THE
AMERICAN NATURALIST

VOL. XLII *June, 1908* No. 498

THE ANCESTRY OF THE CAUDATE AMPHIBIA

DR. ROY L. MOODIE
UNIVERSITY OF KANSAS

THE phylogeny of the group of vertebrates commonly called amphibians or batrachians has been, and still is to some extent, among the most obscure of the problems connected with the descent of animals. So far as I am aware there have been but few statements as to the possible ancestry of the Amphibia and no attempt has been made to set forth in detail the series of structures through which the animals have passed from the beginning of their line to the present. During the course of an extensive investigation on the extinct Amphibia of North America, the writer has reached some interesting conclusions in regard to the ancestry of at least one group of the modern Amphibia and these conclusions are here set forth in detail. Some of the facts offered in support of these conclusions have been given in other connections.

So far as at present known, the first trace of vertebrate life on earth is that of fishes in Ordovician rocks in Colorado and in two places in Wyoming, *i. e.*, the Black Hills and the Big Horn Mountains. In the Devonian, if the impressions from the Catskill are properly interpreted, the fishes had given rise to a quadrupedal type of animals which are usually known as the Amphibia. Only impressions of footprints in the sandstone are known, but these are quite instructive. There are no traces of the bones

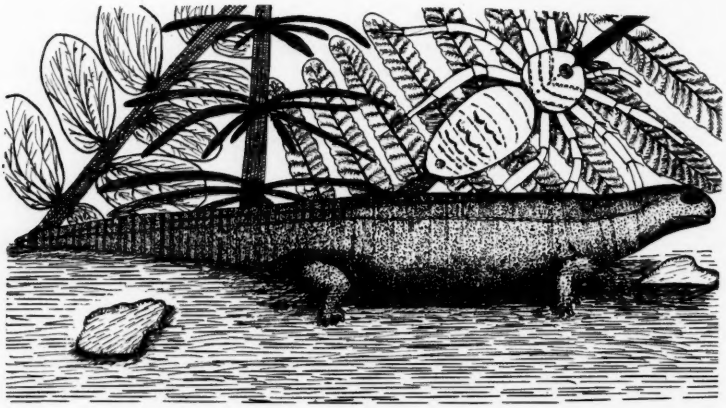


Fig. 1. Restoration of *Micrerpeton caudatum* Moodie from the Coal Measures of Illinois. Length of form, 49 mm. Spider is a composite restoration and is based on actual specimens and on the results of Roemer, Scudder, Beecher and Melander. $\times 2\frac{1}{3}$.

of these quadrupeds known in rocks of Devonian or of Mississippian age, although Lohest (1) some years ago called attention to some remains which he thought were amphibian from the Devonian rocks of France. Thevenin has recently cast doubt upon this interpretation by Lohest (2) and the figures as given by Lohest would seem not to be amphibian, but fish remains.

In rocks of the lower part of the Pennsylvanian occur, in North America, the first evidences of the bones of quadrupeds. The Amphibia show, even thus early, that their line had divided into three and possibly four distinct groups which are usually known as the Branchiosauria, the Microsauria, the Aistopoda and the Stereospondyli. The presence of the last group is indicated by the two vertebræ from the Carboniferous of Nova Scotia named by Professor Marsh *Eosaurus canadensis* and also by certain fragments of large ribs and large skulls from the coal beds of Ohio. The Temnospondyli did not make their appearance until the latter part of the Pennsylvanian, when their remains are found in Carboniferous rocks of Kansas, Illinois and Pennsylvania.

The Stereospondyli and the Temnospondyli are specialized side branches of the amphibian or reptilian stem and will not concern us further here. The Aistopoda are regarded by the writer at present as being specialized microsaurians. This would not favor the view of Wiedersheim as to the descent of the Cœcilians. This point needs further investigation and will be discussed elsewhere. The Microsauria Dr. Gadow has placed in the subclass Proreptiliæ and, in the opinion of the writer, his classification represents the correct facts, but further discussion will be postponed. The group to which the reader's attention is here invited is the one usually known as the Branchiosauria, representatives of which are found only in Western Europe and in North America, where a single specimen is known from Illinois. The group is a very small one both as to the size of the individual members and as to the number of species.

The Branchiosauria are distinguished from all of the other Amphibia-like vertebrates by the presence of short, heavy, straight ribs. The Microsauria always have long, thin, curved ribs. The Aistopoda usually are destitute of ribs or when present they are curved and slight. In conversation recently with Dr. Gadow he made the interesting suggestion that the characters presented by the ribs might be used as a basis on which to separate the group heretofore known as Stegocephala into two main divisions. One of the divisions would be the true Amphibia with the Branchiosauria as the representative order among the early forms, in which case the term Branchiosauria would be a misnomer, and the other Stegocephala would be included under some such name as the Pro-

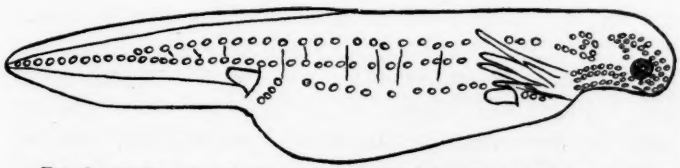


FIG. 2. Outline of a Larva of *Necturus*, showing the arrangement of the lateral line systems. After Platt.

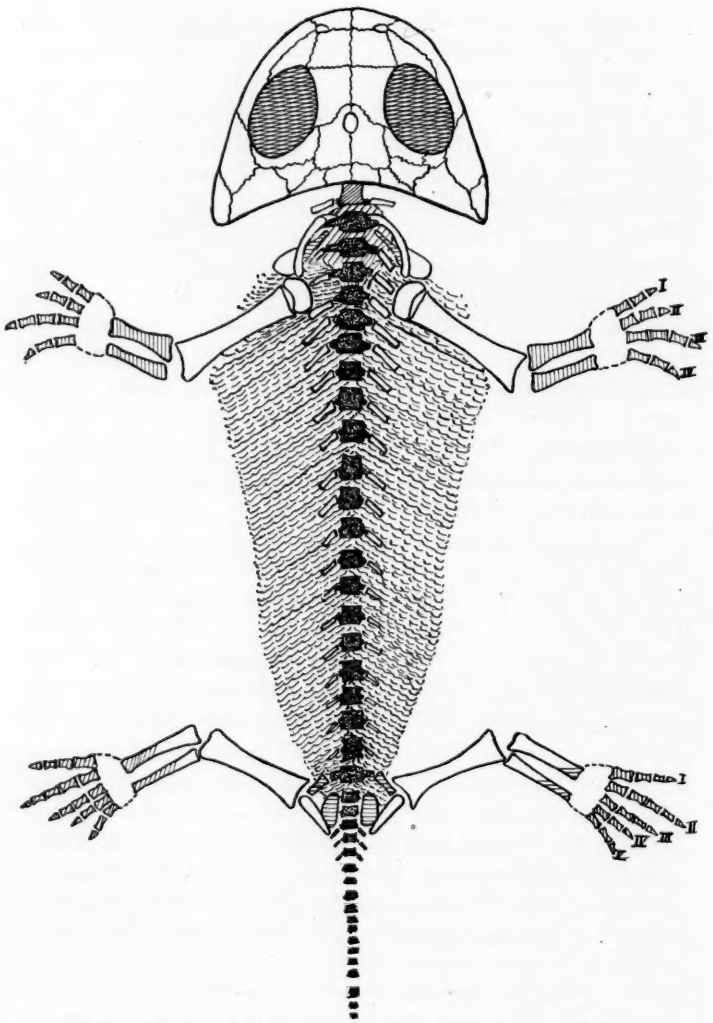


FIG. 3. Restoration of the Skeleton of *Micrerpeton caudatum* Moodie. The feet are conjectural and are based on the studies of Credner. The broad ventral armature is well developed in this form. $\times 3\frac{1}{2}$.

reptilia or would be distributed among the reptiles proper. The former group is characterized by the short straight ribs borne on stout transverse processes and the

latter group is characterized by the long curved ribs borne intercentrally. There seem to be some difficulties in this classification, but it is hoped that they may be cleared up by future investigation.

The Branchiosauria, as has been several times suggested by various authors, represent the ancestral forms of at least the tailed division of the Amphibia. A suggestion as to the ancestry of the tailless forms will be given elsewhere. The conclusion that the Branchiosauria are the direct ancestral forms to the modern Caudata is based on several characters. These characters are: the structure of the skull, the structure and form of the vertebræ and ribs, the number of digits, the arrangement of the phalangeal elements, the characters of the pectoral and pelvic girdles, the character of the lateral line system, the structure and form of the long bones and finally the shape of the body; all of which will be discussed below.

It has been suggested on embryological grounds that the Amphibia are a degenerate group (3) and this is borne out, in so far as the Caudata are concerned, by a study of the cranium of the early and recent forms as well as by other structures. The cranium of the Branchiosauria is almost identical in structure with that of the Microsauria and it exhibits a completely roofed-over skull with only five openings, namely, those for the orbits, the nostrils and the pineal opening.

The elements forming the roof of the skull are quite constant in the Branchiosauria and also in the Microsauria and they differ only in position and relations. Practically the same elements form the skull roof in the two groups, but the forms differ in other important respects. In the skull of the Branchiosauria we find in the median line a row of elements in pairs, which extend the entire length of the skull. These are (beginning anteriorly): the premaxillæ, the nasals, the frontals, the parietals and the supraoccipitals. On the side of these elements lie others which vary in their position to some extent; the median elements are fixed and not so likely to

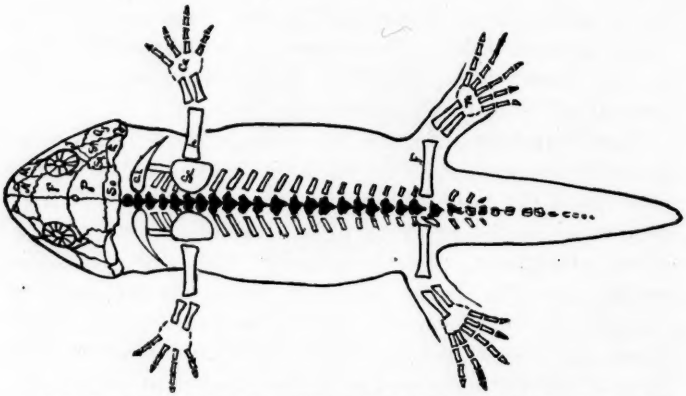


FIG. 4. Restoration with Outline of the *Branchiosaurus fayoli* Thevenin based on the figures given by Thevenin. The last phalanx in digit I of the hand is conjectural and the last two on digit II and the last one on digit IV of the foot are conjectural. From the Upper Carboniferous of France. ×2.

vary. Anterior to the orbit there are the prefrontal, the lachrymal, the maxilla, and lateral to the orbit lies the jugal. Posterior to the orbit lie the postorbital, the postfrontal, the squamosal, the supratemporal, the opiotic, and on the postero-lateral border of the skull lie the quadrato-jugal and quadrate.

In the skull of the modern Caudata we find an arrangement of the elements which is quite similar to that described for the Branchiosauria. In the skull of Megalobatrachus (Fig. 10), for instance, we find the following

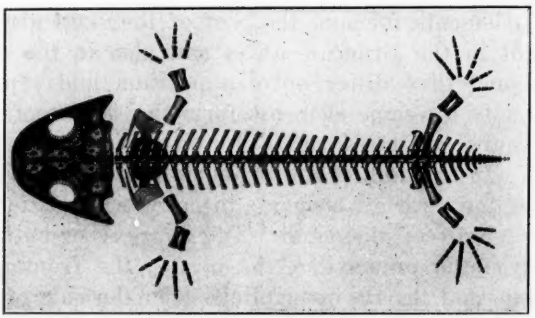


FIG. 5. Restoration of *Branchiosaurus amblystomus* Cred. from the Permian of Saxony. After Credner.

bones paired in the median line: the premaxillæ, the nasals, the frontals, the parietals, and on the posterior end of the skull occur the exoccipitals. In this series it is clear that the supraoccipital elements have disappeared. Lateral to the median paired row there are the maxilla, the prefrontal, the squamosal, and in allied forms the jugal, quadratojugal and quadrate. The epiotic is wanting in all skulls of modern amphibians except some coccidians and the elements are not so firmly united as in the skull of the Branchiosauria. The skull of the Caudata exhibits a weaker, more degenerate condition, than is found among the early forms. The lower surface of the skull is practically the same in the two groups, especially in the possession of a large parasphenoid. Teeth on the palate bones are lacking, for the most part, in the modern forms, which is another evidence of degeneracy.

If the structure of the vertebræ is now examined it will be seen that in this particular there is close affinity between the modern Caudata and the Paleozoic Branchiosauria. The vertebræ of the modern Caudata are amphicœlous and opisthocœlous, with the notochord rarely persistent and with the transverse processes springing off boldly from the body of the centrum. Similar conditions are observed in the Branchiosauria where the vertebræ, so far as they are known, are amphicœlous and the transverse process is unusually strong with the notochord probably persistent. The transverse processes give support to the short, heavy, stout ribs which lay in the flesh and made acute angles posteriorly with the vertebral column. The ribs in the Branchiosauria and in the later Caudata are indistinguishable so far as form is concerned. The point of difference is that in the modern forms the ribs are usually weaker posteriorly and are, for the most part, confined to the presacral region of the body. This is another instance in which the Caudata show their degenerate structure. On the basis of the ribs alone the Branchiosauria may well be separated from the Microsauria and from all other of the so-called Stegocephala, and would be considered as the true Amphibia,

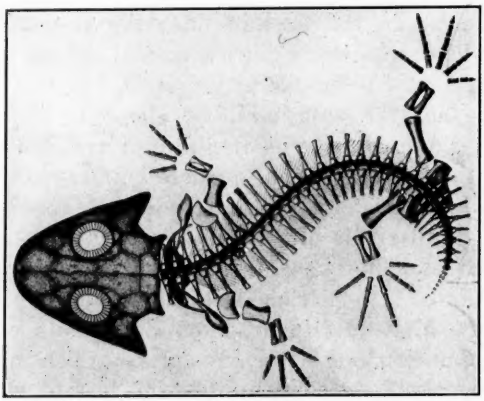


FIG. 6. Restoration of *Melanerpeton* from the Permian of Saxony. After Credner.

while all other forms would be excluded from this class and would have to be placed among the Reptilia, where they probably belong; whether they are to be considered as a subclass of the Reptilia or not, does not concern us here.

In the forelimb there are never more than four digits either in the Paleozoic Branchiosauria nor in the later Caudata. So far as I am aware, there is no paleontological evidence to show that there ever were more than four digits in the hand of the caudate Amphibia and in this discussion the first digit will be considered as No. I., the second digit as No. II. and so on. Fritsch, it is true, has figured five digits in the hand of *Branchiosaurus salamandroides* Fr. (Fig. 7), from the Permian of Bohemia, (4) but in giving us a glimpse into the material on which his restoration is based there are only four digits preserved in the hand, although Fritsch says the first had been lost. I doubt if there ever were more than four, and the digits in Fritsch's specimen were all preserved. In all of the Permian forms from Saxony Credner has figured four digits in the hand (Figs. 5–6).

The specimens recently described by Thevenin from the Upper Carboniferous of France (5) show only four

digits in the hand. In Fig. 4 a restoration of the *Branchiosaurus fayoli* Thevenin has been attempted. The reconstruction is based on the figures as given by Thevenin. Only one phalanx is restored and that is the distal one of the first digit. All of the rest were preserved. In the Wealden of Belgium the *Hylæobatrachus croyii* Dollo (Fig. 8) exhibits but four digits in the hand. In *Andrias scheuchzeri* Tschudi (Fig. 9) from the Miocene of Switzerland, there are but four digits in the hand, and in all of the modern caudate forms, so far as I am aware, there are but four digits and the phalangeal formula for all, both in Paleozoic and in later forms, is universally 3–3–4–3.

In the foot the Branchiosauria show the same agreement with the modern Caudata. There are always five digits and they usually have the phalangeal formula 4–5–4–3–3. Neither the carpus nor the tarsus is fully ossified in the Branchiosauria or in the later Caudata, although the carpus and tarsus are partly osseous in the Amblystomatidæ.

The pectoral girdle of the Branchiosauria consists usually of four elements, three paired and one unpaired. These are: the single interclavicle, the clavicles, the coracoids (cleithra?) and the scapulæ. Among the modern

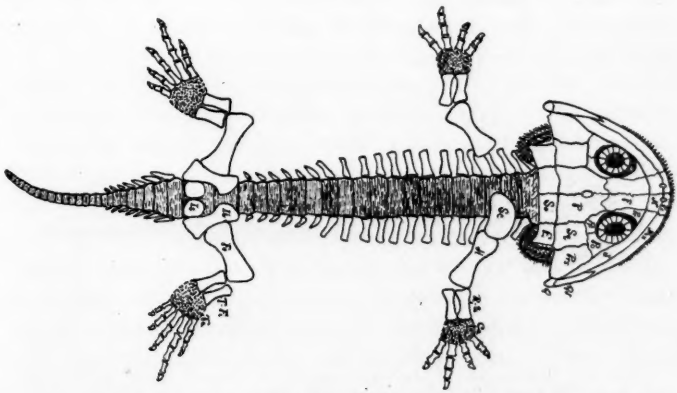


FIG. 7. Restoration of *Branchiosaurus salamandroides* Fr. from the Permian of Bohemia. Modified after Fritsch.

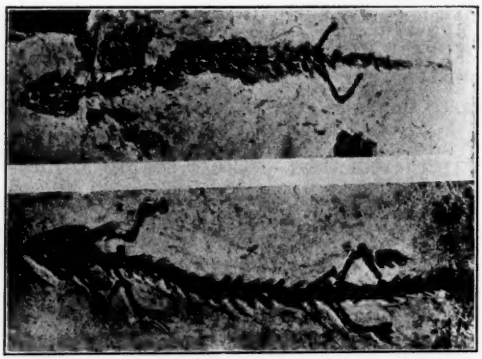


FIG. 8. *Hylæobatrachus croyii* Dollo from the Wealden of Bernissart. After Dollo.

caudate forms as well as among the Miocene forms all of the elements with the exception of the scapulæ have become cartilaginous, so that there remains in the modern caudate amphibians only a bony scapula. This seems to be the case in the Wealden Hylæobatrachus, but the single specimen is not well enough preserved to furnish definite information on this point. The pelvic girdle has, apparently, undergone no change in the evolution of the Caudata. The pubis is never ossified in either the Branchiosauria or in the latter Caudata and the ischium is usually plate-like, while the ilium is more or less rounded. The sacral rib, of which there is never more than one pair, is usually well developed.

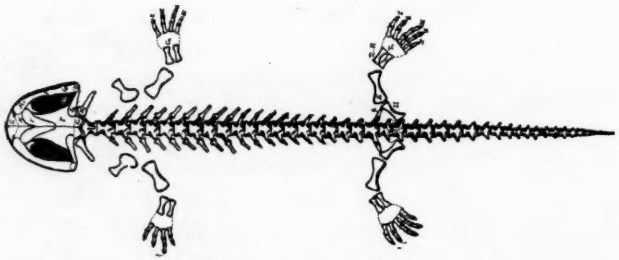


FIG. 9. Restoration of *Andrias scheuchzeri* Tschudi based on the drawings published by von Meyer in "Fauna der Vorwelt." $\times \frac{1}{4}$.

In an essay now in press on "The Lateral Line Organs in Extinct Amphibia" the writer has called especial attention to the character of the lateral line organs as they are preserved in the single specimen of a branchiosaurian, Micrerpeton, from the Coal Measures of Illinois. A restoration of this form has been attempted in Fig. 1. The animal, as preserved, measures only 49 millimeters. It is apparently an adult, as there are no evidences of branchiæ and the limb bones are well formed. The spider shown in the restoration is a composite and is

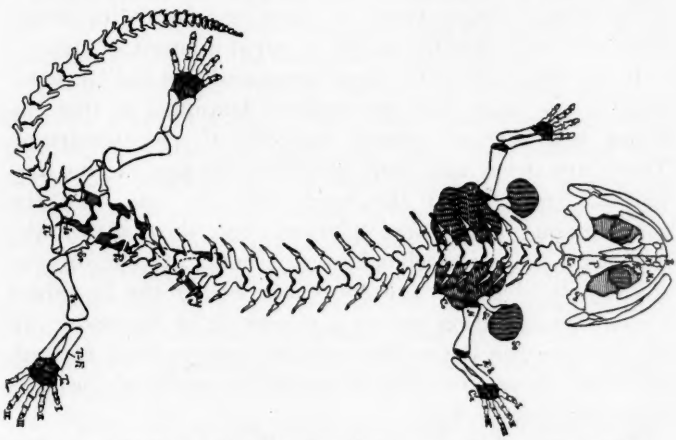


FIG. 10. The Skeleton of *Megalobatrachus japonicus* ——. After Osawa.

based partly on actual specimens partly on the results of Roemer, Beecher, Scudder and Melander. The body of the spider which was used as a model was about a half an inch in length. The particular characters in the amphibian which deserve mention now are the two lines representing the lateral line organs. There is seen a median lateral line which starts at the tip of the tail and runs forward. The other begins somewhat anteriorly and springs boldly from the median lateral line at a distance of a few millimeters from the tip of the tail. These lines represent rows of pigmented scales which show on the

specimen as dark lines. The sense organs were undoubtedly located beneath these specialized scales, much as the lateral line organs are protected in some of the fishes. In Necturus (Fig. 2) the arrangement of the lateral line organs is almost identical with what has just been described for Micrerpeton. I have suggested elsewhere that this similarity in the lateral line organs of these two forms may be indicative of relationship between the groups to which these forms belong. There is no reason why the type of lateral line should not have been preserved in the amphibians, since we know that in some of the fishes certain types of peculiar lateral line structure have persisted for nearly as great a length of time.

In the structure of the limb bones and ribs the Branchiosauria are much like the modern Amphibia in that the bones are formed almost entirely of perichondrium. There are never any bony epiphyses in any of the Amphibia. In some of the toads Parsons has seen the cartilaginous epiphyses calcified, but they are never osseous. The endochondrium is not at all or but slightly developed in the Amphibia, and in the fossilized bones this condition causes a concavity at the ends. In the Microsauria the endochondrium is more fully formed, although there are some in which the ends of the limb bones are nearly flat.

The form of the body in the Branchiosauria is strikingly salamandrine, as may be seen by referring to figures 1 and 4. In Micrerpeton the tail is quite long and almost equals the length of the presacral region. In the *Branchiosaurus fayoli* Thevenin (Fig. 4), the tail is shorter but the form is much the same. The body of the Branchiosaurus (Fig. 4) is more stout than that of the Micrerpeton (Fig. 3) and the ribs are longer.

In summing up all of the characters as presented by the Caudata and the Branchiosauria it seems most probable that the Caudata are but degenerate Branchiosaurians and the changes which have taken place in the skeleton are mostly brought about by the loss of certain parts.

Summary

1. The Stegocephala will probably have to be divided into two groups, one of which will be considered as Amphibia and the members of the other group will have to be placed among the Reptilia but can not all be placed under any single head since they represent divergent types and must be placed in with the reptilian groups to which they have probably given origin.

2. The Branchiosauria are the ancestral forms of at least the caudate Amphibia. The Branchiosauria are first known in the Pennsylvanian of North America and they present characters which separate them clearly from all other groups of the so-called Stegocephala.

3. The characters which the Branchiosauria have in common with the Caudata are: short, straight ribs; stout transverse processes springing from the body of the vertebra; practically the same number of presacral vertebræ; the same skull structure; the degenerate character of the pectoral girdle and the close correspondence of the pelvic girdle; the same number of the digits and the same phalangeal formula in the Branchiosauria and Caudata; the similar characters presented by the lateral line system; the structure of the long bones and the shape of the body.

4. There can be but little doubt that the Caudata are the direct descendants of the Branchiosauria, of which they are but degenerate forms.

Bibliography

1888. Lohest, M. *Annales de la Société Geol. de Belgique*, Tome XV, p. cxx.

1906. Thevenin, A. *Annales de Paleontologie*, Tome I, Fascicule III, p. 13.

1907. Hatta. On Gastrulation in Petromyzon. *Journ. of the College of Science*, Tokyo.

1889. Fritsch, Anton. Fauna der Gaskohle. Bd. II.

1906. Thevenin, A. *Annales de Paleontologie*, Tome I, Fascicule III, p. 9, Plate I.

THE SPIROCHETES AND THEIR RELATIONSHIP TO OTHER ORGANISMS

PROFESSOR HENRY B. WARD[1]

UNIVERSITY OF NEBRASKA

IN Ehrenberg's famous work, "Die Infusionstierchen als vollkommene Organismen," written in 1838, the fourth family of the Vibrionides, or vibrating animalcules, includes five genera which that author regarded as animals and distinguished as follows:

- Segmented threads (monad-stocks)
  - rectilinear (by rectangular transverse fission)
    - non-flexible ..... *Bacterium*
    - serpentine and flexible .. *Vibrio*
  - spirally twisted (by oblique transverse fission)
    - twisted segments flexible ..... *Spirochæta*
    - inflexible
      - cylindrical elongate *Spirillum*
      - discoidal compressed *Spirodiscus*

The details of structure which Ehrenberg had elsewhere worked out with too imaginative industry, he sadly acknowledges are here "barred to our present powers of vision by virtue of their minuteness"; and he is forced to depend upon scanty data to differentiate the to him closely related genera. To-day three among the associated genera are generally recognized as bacteria and of the spirochetes alone is there doubt as to their proper relationship in the systematic tree.

However, Ehrenberg was not the first to observe such organisms. In 1773 O. F. Müller described corkscrew-like animalcules found in foul water, and in 1786 discussed and figured several species, unconscious that in 1777 Köhler had published the first figure of such a form.

[1] Studies from the Zoological Laboratory, The University of Nebraska, under the direction of Henry B. Ward. No. 90.

Yet both descriptions and figures are far too indefinite to permit of more than a guess as to the genus under consideration. Even Ehrenberg's work affords scanty means for the recognition of the forms of which he listed one spirochete and three spirilla. The group, though familiar to all students of microscopic life, has remained only superficially known up to very recent times, in fact until the discovery of the important rôle which certain of them play in the production of disease turned once more the attention of investigators in this direction. Despite the characteristic of flexibility noted by Ehrenberg, and the indifference they displayed towards ordinary methods of bacteriological culture, most authors have grouped these organisms together among the bacteria. Renewed attention to the group served to emphasize at once radical differences of opinion as to its interpretation.

Undoubtedly the impetus to this study was given by Schaudinn's discovery of such an organism in syphilis and the intuitive inference which has been abundantly verified that others would be found in similar relation to diseases as yet entirely unexplained. Working on this and on other species, Schaudinn confirmed the view of Ehrenberg as to the characteristic flexibility of the spirochetes, and determined the occurrence of longitudinal division and the presence of polar flagella, single save just before division. He also demonstrated certain differences between the form found in syphilis and other common spirochetes, which he thought served to justify their generic separation. Throughout he maintained firmly the animal nature of the group.

Almost simultaneously there appeared in 1906 several papers which dealt with the problem as to the nature of this group and arrived at diametrically opposite conclusions. In the first, by the parasitologist Blanchard (1906), was analyzed briefly the morphological basis for the genera of microorganisms in which the body has the form of a spiral. In comparison with these the author

considered very briefly also certain clearly bacterial forms (*Spirosoma, Vibrio, Spirobacillus*) and others distinctly flagellate (*Trypanosoma, Trypanoplasma*) which in his opinion manifest close relationship to the true spiral microorganisms of which he recognized three well-founded genera, *Spirillum, Spirochæta* and *Treponema.* The group of plant organisms he classed as follows:

SPIROBACTERIA Cohn 1875

Bacteria more or less curved in a spiral, the curve forming at times only the arc of a circle, in other cases forming spiral coils more or less numerous. Organisms little flexible or not at all, multiplying by transverse division. Formation of endogenous spores demonstrated in a number of species.

Four genera: *Spirosoma, Vibrio, Spirobacillus, Spirillum.*

Of the last genus he says: *Spirillum* Ehrenberg 1830—Body spiral, cylindrical in transsection, not tapering at the ends. No undulating membrane. One or several flagella bent in a regular curve, either at both extremities or at one only. Formation of endogenous spores demonstrated in a number of species. Organisms relatively of considerable size, cultivated easily on various media used in bacteriology.

The spirilla are clearly bacteria. They live as saprophytes in wells, stagnant waters, the soil, liquid manure, etc., and generally in media very poorly oxygenated. Possibly one should include in this genus some forms which are found in pus, but it is doubtful if these play an active part in it, and up to the present time not a single species can be considered as surely pathogenic.

Over against these forms, and sharply contrasted with them Blanchard placed the animal organisms of a general spiral form. These he included in a single family, characterized thus:

TRYPANOSOMIDÆ Doflein 1901

Flagellates twisted into a spiral, the coils being more or less numerous. Organisms flexible, with form more or less fixed, multiplying by longitudinal division. No endogenous spores. Locomotive apparatus consisting either simply of an undulating membrane, or of such a membrane together with one or two flagella. Not stained by Gram's method, not cultivated in the media used in bacteriology.

Four genera: *Spirochæta, Treponema, Trypanosoma, Trypanoplasma.*

The first two genera are very similar and include the only forms concerning the animal nature of which there is any question. It will be necessary to consider these somewhat closely. The first is characterized thus:

SPIROCHÆTA[1] Ehrenberg 1833

Body excessively slender, spiral, flattened, ectoplasm extending in a narrow undulating membrane which surrounds in a spiral the entire body. No flagella, no endogenous spores. Nucleus greatly elongated, filiform, in the axis of the body, with chromatin granules distributed along its surface. Reproduction in all probability by longitudinal division. None of the media used in bacteriology serve to maintain cultures of these organisms. Type species, *S. plicatilis.*

All these forms are by some students assigned to the bacteria. Some species are inhabitants of stagnant waters, others live in the sea or in decaying organic materials, while still others are parasitic. Among the latter are forms recently recognized as the cause of most virulent infective diseases in man and other animals. The genus characters given above are not in their original form, but as emended by Blanchard, and this emendation becomes now the basis of the group thus named. The emendation is based primarily upon the epoch-making investigations of Schaudinn.

[1] The name is often written *Spirochæte,* which does not conform to rules of Latin or of nomenclature.

Blanchard lists in this genus the following species:

1. *S. plicatilis* Ehrenberg 1833, from stagnant water.
2. *S. buccalis* Cohn 1875, from the buccal cavity.
3. *S. obermeieri* Cohn 1875, from the blood of man in cases of relapsing fever. The possible varieties of this species, found in various types of relapsing fever, are also noted.
4. *S. dentium* Koch 1877, very small species from the mouth.
5. *S. gigantea* Warming 1875, from brackish water.
6. *S. eberthi* (Kent 1880), from the intestine of birds.
7. *S. balbianii* (Certes 1882), from the intestine of lamellibranchs.
8. *S. anserina* Sakharov 1891, cause of septicemia in birds.
9. *S. theileri* (Laveran 1903), from blood of cattle.
10. *S. pyogenes* (Mezincescu 1904), from pus in a case of pyelitis.
11. *S. gallinarum* R. Blanchard 1905, cause of septicemia among chickens.
12. *S. refringens* Schaudinn 1905, from lesions of syphilis.
13. *S. pertenuis* Castellani 1905, from lesions of yaws.
14. *S. ovina* R. Blanchard 1906, from blood of sheep.
15. *S. vincenti* R. Blanchard 1906, from abscesses in man.

Also several other uncertain forms.

It is evident that this assemblage of forms is not entirely natural. Of many little is known beyond the size and manner of life. The latter presents radical differences, but the formation of new genera on purely physiological grounds is recognized as a most dangerous procedure. No doubt better knowledge, especially of the life cycles, will lead to the removal of groups of these species to new genera, but such must be based upon distinctive characteristics; any other method only results in greater confusion. New forms are being described constantly, *e. g., S. lymphatica,* which White and Proescher regard

as the cause of a lymphatic spirillosis; it stains like *Treponema pallidum.* More extended investigation alone will justify assigning a definite place to such organisms. Yet apparently the group of spirochetes producing relapsing fevers may justly be made an independent genus, even though their morphological differentiation is difficult. They constitute the newly created genus.

SPIROSCHAUDINNIA Sambon 1907

Blood parasites only imperfectly known. In blood of vertebrate host, they appear as minute, wavy or spiral threadlike bodies. With undulating membrane but no flagella. Free stage alternates with intracellular resting stage with parasite coiled up in host cell. Sporogony in ticks. Stages have been demonstrated in ova, showing the hereditary transmission of the infection. This is contrary to known facts regarding bacteria. Type species, *Spiroschaudinnia recurrentis.*

This genus is as yet not clearly differentiated from *Spirochæta* and may ultimately prove to be synonymous with it. The presence of an intracellular stage and the mode of infection through biting insects are the slender basis on which it rests at present.

In this genus Sambon has included two forms which produce relapsing fevers in man. One is *S. recurrentis* (Lebert 1874), better known by the synonym *Spirillum obermeieri* Cohn 1875, which is the cause of the relapsing fever common in Russia, the Balkan Peninsula, Turkey, Persia and India, and known by sporadic cases over the entire world. Patton has shown that the parasite is transmitted by the common bedbug (*Acanthia lectularia*) and possibly by the body louse (*Pediculus vestimenti*), although the evidence is not conclusive. The second species, *S. duttoni,* the cause of African relapsing fever, is difficult to distinguish morphologically from the foregoing, but is shown by experiment in animals to be distinct from it. According to Dutton and Todd the organism is transmitted by the tick, *Ornithodoros moubata*

(Murray). The young of infected ticks are capable of inoculating the disease and the spirochætes have been found in the eggs, where in fact they multiply and thus infect the new generation. This is evidently true hereditary transmission of disease.

A third species should be added to this genus, namely, the organism producing the relapsing fever of Bombay which Novy and Mackie have shown by inoculation experiments to be distinct from either of the preceding forms. To this form the name *Spiroschaudinnia carteri* has recently been given by Mackie. The disease caused by this species has been transmitted experimentally by a grooved needle and also by the bedbug, and none of the experimental animals contracted the disease in any other way than by inoculation.

In his outline Blanchard included one other genus, which with its diagnosis is as follows:

TREPONEMA Schaudinn 1905

Spiral body not flattened, but cylindrical in transsection, tapering towards the extremities. One flagellum at each extremity, no undulating membrane. Multiplication by longitudinal division, the initial stage of which may be identified by the doubling of the flagellum at one of the ends. Division forms remain long attached by their ends. Type species; *T. pallida.* One of the marked characteristics of this spirochete is the resistance to ordinary methods of staining. This stands in sharp contrast to conditions among bacteria. Gram's method and many others do not stain it at all, while no stain colors it deeply.

This form was discovered by Schaudinn and Hoffmann in syphilitic lesions; it has been experimentally transferred to apes, with the result of producing characteristic signs of the disease and has not been found in other diseases. Another species, *T. pertenuis* (Castellani 1905), which is regularly associated with the tropical disease known as frambœsia, or yaws, also belongs here.

But even after these forms have been removed Blanchard's original list of the genus *Spirochæta* still shows an unnatural mixture of varied forms. Among the remaining species are undoubtedly those which form other natural groups and will later be assigned to new genera; but in the absence of fuller knowledge they may preferably be left for the present in the old genus. No doubt new forms will be added to this list. In this connection attention should be called to yellow fever and the view often expressed that the yet unknown cause of this disease will also prove to be a spirochete. Similarly the Miana disease of Persia known to be transmitted by a bird tick, Argas persicus, and other tick diseases in tropical and subtropical countries are thought to be due to the inoculation of closely related organisms.

Only two weeks later than the publication by Blanchard appeared an extensive paper by Novy and Knapp (1906). These authors recorded studies on a spirochete from a case of relapsing fever which was observed in Bellevue Hospital, New York. They regarded this form as identical with *S. recurrentis* and as the result of most careful studies reached the conclusion that the organism in question was undoubtedly a bacterium and not a protozoon. Their figures show strong evidence of transverse division and fail to indicate any trace of bodies which might be interpreted as nucleus, blepharoplast, or undulating membrane. They indicate also the presence of a single flagellum at one end of the spiral about as long as the spiral itself and with wavy turns corresponding in general to those of the spirochete, while a short process occurs at the other end. The staining qualities of the flagellum, the action of the organism under the influence of plasmolytic changes, its behavior both during and after being killed by heat and also the persistence of the spiral form under the most varied injurious conditions, are incompatible, in their opinion, with a protozoan nature and indicate affinity to the bacteria. The readiness with which these authors established active immunity is of-

fered as additional proof of the bacterial nature of the form with which they experimented, and finally they record the absence of a tendency to form layers around each air bubble, which is a very characteristic reaction for trypanosomes. Novy and Knapp conclude thus:

"The several facts which have been brought out under the preceding headings point clearly to the non protozoal nature of *S. obermeieri*. We must conclude, therefore, that the *S. obermeieri* belongs to the bacteria and more especially to the Spirillaceæ. As pointed out, the same conclusion has been reached by Borrel as regards *S. gallinarum* and *S. duttoni*. Three typical spirochetes are therefore demonstrated to belong to the group of bacteria.

"Hitherto it has been assumed that insect transmission indicates a protozoal organism, and in so far as the spirochetes are concerned, the chief evidence which can now be adduced in support of their animal nature is the fact of such transmission in the case of *S. duttoni* and *S. gallinarum*. The facts brought out in this study point so conclusively to the bacterial nature of the organisms that there can be little or no doubt of the correctness of the conclusion arrived at. With the recognition of this proof it follows that insect transmission is no longer a criterion of the nature of an organism."

Radical as is this critique of the animal theory of spirochete relationship, it has not been accepted as deciding the question, and has only provoked further discussion of the problem. Referring first to the question of insect transmission, it may be said that Koch has shown that the spirochetes multiply in the eggs of ticks and Carter that they undergo there changes as yet unexplained which may substantiate the claim of another cycle. Several investigators have found that in experimental animals they pass through the placenta from the maternal circulation to the fetal, although they undergo no changes consequent to this transfer. These observations do not accord with known facts concerning other bacteria.

Almost at the same time there was published an exceedingly careful investigation into the structure and development of the fowl spirochetes by Prowazek, with an appendix on a species from *Anodon* by Keysselitz, in which both authors come to conclusions diametrically op-

posed to those of Novy and Knapp with regard to the structure and relations of the spirochetes. It should be remembered that the species (*S. gallinarum*) on which Prowazek worked was one of those which Novy regarded as most positively of plant affinities. On the basis of most critical observations Prowazek indicates the presence of an undulating membrane with a conspicuous marginal cord. The body of this spirochete he finds to be flexible, a feature emphasized by various authors in the diagnosis of the genus. An analysis of the various types of movement shows, in his opinion, marked similarity to organisms possessing an undulating membrane or to the similarly provided sperm cells. Distinct granules lie in the axis of the organism which do not constitute a definite nucleus in the general sense of the term, but form chromidia such as are well known to occur frequently in the protozoon cell in the place of a single circumscribed nucleus.

So far as the conduct of these spirochetes towards reagents is concerned, the use of salt solutions did not produce the plasmolysis characteristic for bacteria even though the solutions were stronger than those sometimes successful in effecting this among the bacteria. Dilute alkaline solutions affected the spirochetes whereas the bacteria are very resistant towards them.

The identification and interpretation of the method of division is believed to be of especial importance in determining the systematic position of the spirochetes. In the opinion of Prowazek transverse division may occur, yet positive evidence demonstrated the occurrence of longitudinal division. Similar conditions in part were found on the species from the mouth (*S. dentium*), and were especially clearly illustrated by the observations of Keysselitz on a spirochete obtained from the fresh water mussel. Here the character of the undulating membrane and of the chromidia, the conduct of the chromatin granules in advance of division and the essential features of that process which was clearly longitudinal could be

most distinctly observed and delineated. Finally Prowazek calls attention to various protoplasmic accumulations or globules which make their appearance at certain times and in his opinion are not mere products of regeneration, but represent special resting stages in which protoplasm and chromatin granules experience involution. These peculiar processes have also been observed by other investigators on other species and may possibly be interpreted as particularly related to the sexual cycle.

Prowazek concludes that as regards the systematic position of the chicken spirochete (*S. gallinarum*), one is compelled on the basis of the structure, relation to reagents, manner of plasmolysis, and also on the basis of temporary cell parasitism to place the species among the protozoa and in close proximity to the trypanosomes. The undulating membrane was observed by Schaudinn in *S. dentium, refringens* and *ziemanni*. The existence of this structure can no longer be questioned. The large form discovered by Keysselitz suggests the large *S. plicatilis* and forms the transition to *S. balbianii* of the oyster which is without doubt closely related to the trypanosomes.

In a very recent paper Fantham (1908) demonstrates the occurrence and character of the spiral membrane in *S. balbianii* and *S. anodontæ*. He also explains the character of the movement as due to myonemes in the spiral membrane. Longitudinal division he finds to be frequent and to involve first the basal granules, then the membrane, next the chromatin masses and finally the body, the halves of which subsequently remain attached end to end. Fantham sees no clear evidence of sexual dimorphism, and finds the spirochætes non-plasmolyzable and without aerobic reactions. As characters manifesting bacterial affinities he lists the diffuse nucleus like spirilla; transverse fission even though infrequent, and the absence of a blepharoplast. Features suggesting protozoan affinities are the possession of a membrane, longitudinal fission, their non-plasmolyzable character

and several minor or doubtful factors. The spirochetes he believes to be distinct from trypanosomes in their less highly specialized structure, which exhibits morphological resemblance to bacteria.

In the face of such conflicting testimony on these morphological and physiological factors of primary importance for the interpretation of the group, one is compelled to seek collateral evidence to see if any can be secured which is definite, even though not in itself decisive. A few such indications are to be found among the uncontroverted records of various investigators. It is noteworthy that spirochetes resist culture in the media which serve readily for bacteria in general, and herein also resemble other protozoan saprozoites.[2]

Among indirect evidence one should note the work of Marchoux.[3] It has been observed that spirochetes easily lose their virulence. This author found that *S. gallinarum,* if passed through a series of birds, loses its lethal power and infectivity. In nature, however, the disease maintains its virulence, destroying entire broods in countries where it is endemic. The persistent virulence is thus seen to be related to the transmitting agent, the tick *Argas miniatus.* However, these ticks are incapable of increasing the virulence of a strain that has become attenuated and merely maintain any strain at its own level. These conditions do not resemble the action of bacteria, but, on the other hand, do simulate the conduct of protozoa, which pass through part of the life cycle in an intermediate host.

Another indication of much importance was furnished by Lingard in 1903 when he observed spirochetes in cattle penetrating red blood cells. Prowazek describes and figures in detail this occurrence in the fowl's blood where the parasite, after entering the corpuscle assumes a coiled or resting condition which he believes related in some manner to the (supposed) developmental cycle in the

[2] This convenient term introduced by Blanchard indicates at sight its meaning through analogy with the well-known botanical term, saprophyte.

[3] *C. R. Soc. Biol.,* 62, October 12, 1907.

intermediate host (*Argas*). Very recently Balfour (1907) has seen the spirochete actually enter the red corpuscle, and undergo changes within it in which the chromatin core is broken up into separate globules. This stage is very difficult to stain and has hitherto escaped emphasis. Some observers believe it to represent degeneration changes; even then it is incompatible with the theory of bacterial relationship, while, on the other hand, it suggests strongly conditions which prevail among other hematozoa. One is forced to note its great resemblance to the "latent body" of trypanosomes recently described by Moore and Breinl. This consists of a nucleated fragment of protoplasm which is stored up in spleen and bone marrow of infected animals and ultimately reappears in the circulation when it gives rise to a new trypanosome.

Jaffé (1907) has studied a form (*S. culicis*) found in mosquito larvæ and gives a careful analysis of the motile phases which stand in sharp contrast with the stiff screw movements of spirilla. He emphasizes also the ribbon-shaped body, the great susceptibility to solution of KOH even thougl. very dilute, the axial nuclear (?) thread, and the occurrence of both transverse and longitudinal division.

The last work by Dutton and Todd (1907) demonstrated for *S. duttoni* a ribbon-shaped body with a central deeply staining core and a lighter periplastic sheath which at one end at least is prolonged into a flagellum. The central core does not stain uniformly, but has unstained areas and is sometimes broken up into granules. While these organisms occur singly, chains of three or four are frequent. They usually multiply by transverse fission, but longitudinal division also occurs periodically. Many forms taken from spleen and bone marrow are tightly coiled and a few of these undergo remarkable changes there. In the tick involution changes were observed including fragmentation of the chromatin. This process takes place in the Malpighian tubules where ap-

parently, the bodies burst and the granules become free to form the starting point for a new generation.

The group is evidently a doubtful one even yet. The occurrence of chains and of transverse division strongly favors a bacterial interpretation, but on the whole the trend of recent investigation has been to indicate its protozoan affinities and away from the earlier view of bacterial relationship. The spirochetes are certainly distinct from the spirilla and whether they are ultimately placed among bacteria or protozoa, it seems clear that they will occupy a more isolated position than has previously been assigned them by the advocates of either view. On the other hand, the recent proposal of Fantham to create for them a new group, the Spirochætacea, midway between the protozoa and the bacteria, can not be regarded as a helpful move. Such proposals in other groups have been found on later study to be evidence of an insufficient knowledge of the forms under consideration. Further investigation into the life history will undoubtedly furnish the definite evidence for a decision of the question.

WORKS CITED

1908. Balfour, A. Spirochætosis of Sudanese Fowls—An "After-phase." *Jour. Trop. Med.*, 11, p. 37.

1906. Blanchard, R. Spirilles, Spirochetes et autres micro-organisms à corps spirale. *Arch. de Parasitol.*, 10, pp. 129–149.

1907. Dutton, J. E., and Todd, J. L. A Note on the Morphology of *Spirochæta Duttoni*. *Lancet*, 2, pp. 1523–1525. (Nov. 30.)

1908. Fantham, H. B. *Spirochæte* (*Trypanosoma*) *balbianii* (Certes) and *Spirochæta anodontæ* (Keysselitz): their Movements, Structure and Affinities. *Quar. Jour. Micr. Sci.*, 52, pp. 1–74; 3 pls., 11 text figures.

1907. Jaffé, J. *Spirochæta culicis* nov. spec. *Arch. für Protistenkunde*, 9, pp. 100–107; 1 pl., 2 text figures.

1906. Novy, F. G., and Knapp, R. E. Studies on *Spirillum Obermeieri* and Related Organisms. *Jour. Infect. Dis.*, 3, pp. 291–293; 7 pls.

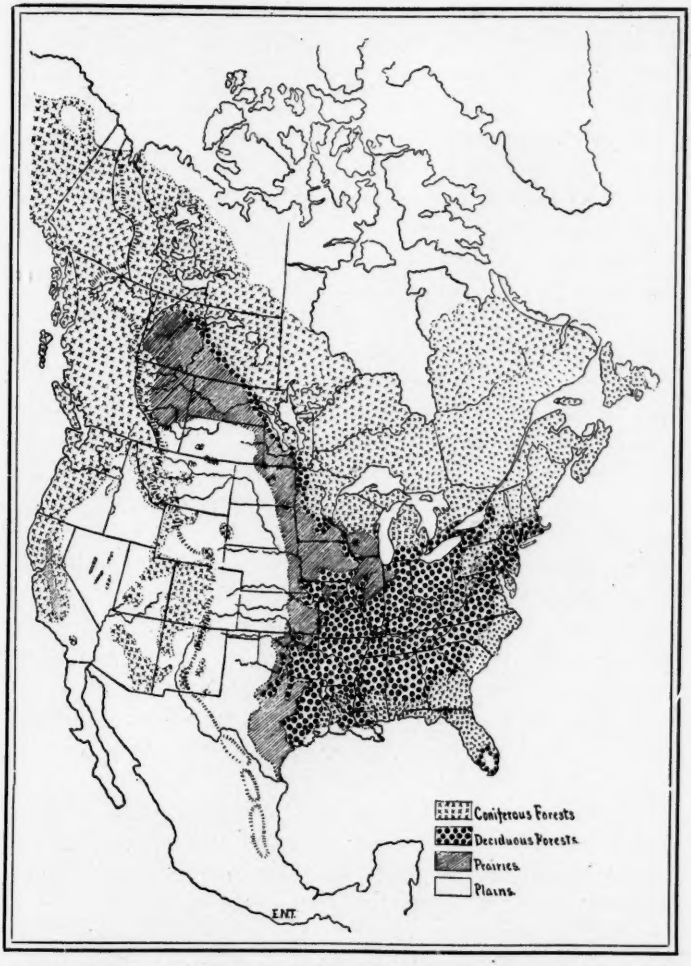
1906. Prowazek, S. v. Morpnologische und entwicklungsgeschichtliche Untersuchungen über Hühnerspirochaeten. *Arb. kais. Gesundheitsamte*, 23, pp. 554–569; 2 Taf.

THE FAUNAL AFFINITIES OF THE PRAIRIE REGION OF CENTRAL NORTH AMERICA

DR. ALEXANDER G. RUTHVEN
UNIVERSITY MUSEUM, UNIVERSITY OF MICHIGAN

THOSE who are acquainted with the literature of the field zoology of North America are familiar with the fact, that, from the time of the Pacific Railroad surveys, naturalists have noted that there are in North America several well-defined biological regions. These have been pointed out at various times by Allen, Cope, Merriam and others, and the fauna of each has been more or less investigated. Of late years there has been a tendency among biologists to discredit this kind of work, owing to the apparent tendency of some naturalists to consider the mapping of these regions as an end in itself, but it seems to me that this work, if done properly, has a very real value.

If it is true that the formation of species among vertebrates is orthogenetic, as Whitman (1907) holds for pigeons, and I have found to be true in the garter-snakes (Ruthven, 1908), and these species are associated with different sets of environmental conditions, as seems to be the case, for example, in the genera Leptinotarsa (Tower, 1906) and Thamnophis (Ruthven, 1908), it is manifestly of importance that these areas of characterization be determined. Certain it is that the areas of characterization will not be the same for all animals, for the reaction of any form to any set of environmental conditions depends fundamentally upon the constitution of the animal, and this is a variable. On the other hand, in the case of terrestrial vertebrates, there would seem to be enough similarity in their mode of life to render



Map showing the location of the plains, prairie, and eastern forest regions of North America. (From Transeau, after Sargent.)

them subject to the same general conditions; a fact that is borne out by faunal studies. For example, we have forms of birds, reptiles and mammals characteristic of the plains region, others characteristic of the south-

eastern deciduous forest region, and still others characteristic of the northeastern coniferous forest region, etc. For these reasons it seems to me that careful faunal studies must contribute very materially to our knowledge of the affinities and relationships of forms.

Among the biotic regions that have been recognized in North America, the prairie region is one of the most interesting. It consists in general of a narrow zone separating the eastern forest from the semi-arid plains, as shown on the accompanying map. In Iowa, Illinois, northern Missouri, and southern Minnesota and Wisconsin, it widens into a wedge that extends to the western boundary of Indiana. Pound and Clements (1900), Transeau (1905), Bray (1901) and Sargent (1884) have shown that both the environmental conditions and the flora of this region are characteristic, but so far as I know the vertebrate life has never, as a whole, received examination.

During the past summer, the writer conducted an expedition[1] for the University Museum, University of Michigan, to northwestern Iowa, for the purpose of investigating the fauna of that region. The collections obtained by this expedition furnished a very representative series of the vertebrates of the prairie region, and a careful study of the data seems to lead to three fundamental conclusions.

1. *The peculiar environmental conditions of the prairie region have an effect upon the vertebrate fauna.* This is shown by the fact that many groups become modified as they enter this region from the adjoining ones. Note the following examples:

(*a*) I have elsewhere shown that as the snake *Thamnophis radix* (B. & G.) enters the prairie region from the plains it becomes strikingly dwarfed.

(*b*) Again, many of the plains forms are replaced in the prairie region by nearly related forms whose principal range is to the eastward of the prairie, as shown by the following instances:

[1] Detailed reports will appear upon the results of this trip.

Plains	Prairie
Western yellow-thoat, *Geothlypis trichas occidentalis* Brewst.	Northern yellow-thoat *Geothlypsis trichas brachidactyla* (Swains.).
Pallid horned lark, *Otocoris alpestris leucolaema* (Coues).	Prairie horned lark, *Otocoris alpestris practicola* Hensh.
Western grasshopper sparrow, *Coturniculus savannarum bimaculatus* (Swains.).	Grasshopper sparrow, *Coturniculus savannarum passerinus* (Wils.).
Sennett nighthawk, *Chordeiles virginianus sennetti* (Coues).	Nighthawk, *Chordeiles virginianus* (Gmel.).
Pocket gopher, *Geomys lutescens* Merriam.	Pocket gopher, *Geomys bursarius* (Shaw).

(*c*) Furthermore many of the forms from the eastern forest region are here replaced by others whose principal range is to the westward of the prairie. The following examples may be noted:

Eastern Forest	Prairie
Garter-snake, *Thamnophis sirtalis* (L.).	Red-sided garter-snake, *Thamnophis sirtalis parietalis* (Say).[2]
Blue-tailed skink, *Eumeces fasciatus* (L.).	Northern blue-tailed skink, *Eumeces septentrionalis* (Baird).
Long-billed marsh wren, *Telmatodytes palustris* (Wils.).	Prairie marsh wren, *Telmatodytes palustris iliacus* Ridg.
Chickadee, *Parus atricapillus* Linn.	Long-tailed chickadee, *Parus atricapillus septentrionalis* (Harris).
Meadow lark, *Sturnella magna* (Linn.).	Western meadow lark, *Sturnella magna neglecta* (Aud.).
House wren, *Troglodytes aëdon* Viell.	Western house wren, *Troglodytes aëdon parkmani* (Aud.).

2. *Most of the forms which inhabit the prairie region either extend also into the eastern forest region or into the plains region, or rarely both, few*[3] *being confined to*

[2] It is uncertain just which one of the Hog-nosed Snakes (*Heterodon*) is to be considered characteristic of the prairie region. *H. platyrhinus* Latr. has been recorded from the prairie region, and even from the plains, but the museum expedition only found *H. nasicus* B. & G. in western Iowa (Clay and Palo Alto Counties). The question can only be settled by detailed collecting and by the careful determination of the specimens.

[3] The pocket gopher, *Geomys bursarius* (Shaw), and the prairie hen, *Tympanuchus americanus* (Reich.), are exceptions to this rule, both being principally confined to the prairie region.

the prairie region. This composite nature of the prairie fauna may be seen by comparing the two lists above.

3. *There is a great difference in the extent to which the forms of eastern North America push westward, or the plains forms push eastward, into the prairie region before becoming modified or checked.* Among the plains forms the Arkansas kingbird (*Tyrannus verticalis* Say) and the western hog-nosed snake (*Heterodon nasicus* B. & G.) only extend into the western part of Iowa, Palo Alto County, being apparently the most eastern authentic locality recorded,[4] but the yellow-headed blackbird, *Xanthocephalus xanthocephalus* (Bonap.), and red-sided garter-snake, *Thamnophis sirtalis parietalis* (Say), extend into Illinois. Again, the prairie hare (*Lepus campestris* Bach.) and others only enter the western part of Iowa, while the Franklin spermophile, *Citellus franklini* (Sabine), penetrates eastward as far as Illinois, and the thirteen-lined spermophile, *Citellus tridecemlineatus* (Mitch.), extends to southeastern Michigan.[5]

Among the eastern forest forms, the Michigan mouse, *Peromyscus michiganensis* (Aud. & Bach.), cotton-tail, *Sylvilagus floridanus mearnsi* Allen, green snake, *Liopeltis vernalis* (De Kay), bluebird, *Sialia sialis* (Linn.), Baltimore oriole, *Icterus galbula* (Linn.), orchard oriole, *Icterus spurius* (Linn.), bob-white, *Colinus virginianus* (Linn.), swamp sparrow, *Melospiza georgiana* (Latr.), and others extend westward at least as far as the western margin of the prairie, while the Butler garter-snake, *Thamnophis butleri* (Cope), garter-snake, *Thamnophis sirtalis* (L.), meadow lark, *Sturnella magna* (L.), long-billed marsh wren, *Telmatodytes palustris* (Wils.) and many other forms, only enter its eastern border.

[4] The University expedition found the Arkansas Kingbird in Palo Alto County, and *Heterodon nasicus* on the line between Clay and Palo Alto Counties.

[5] Mr. P. A. Traverner has recently presented to the University Museum a specimen of *Citellus tridecemlineatus* (Mitch.) from Port Huron, Michigan, and Mr. N. A. Wood, of the University Museum, has observed a specimen in Oscoda County.

These facts, it seems to me, point strongly to the conclusion, that, as far as terrestrial vertebrates are concerned, the intermediate character of the environmental conditions makes of the prairie region an extensive area of transition between the plains and eastern forest regions, but that the environmental conditions are not either intensive or extensive enough to mold the forms into a peculiar fauna.

REFERENCES.

1901. Bray, W. L. The Ecological Relations of the Vegetation of Western Texas. Bot. Gaz., XXXII, 99–123, 195–217, 262–291.

1900. Pound and Clements. The Phytogeography of Nebraska, Lincoln.

1908. Ruthven, A. G. Variations and Genetic Relationships of the Garter-snakes. Bull. U. S. Nat. Mus., 61. (In press.)

1906. Tower, W. L. An Investigation of Evolution in Chrysomelid Beetles of the Genus Leptinotarsa. Carnegie Inst., Pub. No. 48.

1905. Transeau, E. N. Forest Centers of Eastern America. AMER. NAT., XXXIX, 875–889.

1884. Sargent, C. S. Forests of North America. 10th Census ot the U. S.., IX.

1907. Whitman, C. O. The Origin of Species. *Bull. Wisc. Nat. Hist. Soc.*, V, 6–14.

PHYSIOLOGY[1]

PROFESSOR FREDERIC S. LEE

COLUMBIA UNIVERSITY, NEW YORK CITY

IN the introductory lecture of the present course we were told that ours is the golden age of mathematics. As week after week has passed by since then, we have been led from one golden age to another, convinced, for the time, that the present brilliant achievements of each science outshine those of all the others. A few days ago I found on my desk an entomological monograph, the opening sentence of which reads, "The present age is the age of insects." I shall not attempt to harmonize the declarations of my Columbia colleagues with that of my entomological friend. But I feel that I should be derelict in my devotion to my own subject if I did not state frankly at the outset of my lecture—what ought, however, to be a self-evident truth—that the present is preeminently the age of physiology. Nor, following again the example of my predecessors, need I be over-modest in my claims as to the place of physiology in the scientific hierarchy. For Fick speaks of it as "the highest and most fruitful generalization of the collective natural sciences," and Czermak calls it "the summit of all the sciences."

It need not be emphasized that no exact boundary line exists for any one of the biological sciences. The proper domain of each extends, at its borders, imperceptibly into the domains of all, and within the boundary zones it is difficult to say what belongs to one and what to another. With this in mind it is impossible sharply to delimit the science of physiology. Nevertheless its proper domain is

[1] A lecture delivered at Columbia University in the series on Science, Philosophy and Art.

easily surveyed. Physiology deals with the process of life, the living of living substance. It is a dynamic, not a static science. The form, structure and composition of living things do not properly come within its scope: they form the subject matter of morphological, static sciences. But the changes in form, structure and composition, which are manifestations of the life process, are proper subjects of physiological study. Its material exists wherever life exists. Whether it be the growth of a man or of a tree, the creeping of an amœba or the contraction of a muscle, the beating of a heart or the production of a disease by a bacterium, the mental activity of a brain or the response of an infusorian to light, the process of reproduction or of inheritance, the phenomena of nutrition or the behavior of an organism to changes in its environment—all of these and a thousand others are physiological phenomena and proper subjects of investigation in the physiological laboratory. It is true that many departments of learning, which essentially are branches of physiological science, have been so far specialized in the methods of their pursuit and their aims and augmented by non-physiological additions, as to entitle them to specific names. In such cases it often is not expedient for physiology to busy itself with the more remote results of the operations of its laws. The great biologist of the last century, Johannes Müller, was wont to say, "*Psychologus nemo nisi physiologus.*" But, although psychic phenomena are inextricably linked with neural processes, the right of psychology to be recognized as an entity, with the study of psychic phenomena as its prerogative, has been abundantly demonstrated by its achievements. So, too, the proceedings of human society are the resultants of the action in human beings of physiological principles. But the study of the resultants themselves falls within the special province of the sociologist. It is thus customary to recognize as largely independent sciences, such branches of knowledge as psychology, sociology, neurology, biological chemistry, exper-

imental zoology, hygiene, bacteriology, pathology and preventive medicine; but in all these there is a large element of pure physiology, and their adherents often deserve the name of physiologists. When I say that the present is preeminently the age of physiology I mean it seriously, since at no time has the physiological spirit, the spirit of examining vital phenomena by the aid of experimentation, so completely permeated and vitalized the biological sciences as now.

There exist many misconceptions regarding the subject matter and scope of physiology. In the popular mind physiology deals with the life processes of the human body. In reality human physiology is but one of its many interests. It has its anthropocentric aspect. Biocentric it is in reality. The popular conception of physiology as a science of the functions of gross anatomical organs expresses, too, but a small part of the truth. During the middle part of the last century a powerful school of investigators in Germany busied themselves largely with the functions of organs, and strongly impressed the science of their time and the popular mind. But one of the pronounced phases of physiological development in recent years has been a similar rich growth of the study of the life processes of the cell. Another popular misconception is that physiology deals only with the internal parts of organisms—a view that is confuted by the fact that there is now going on much investigation of the mutual relations of organisms and their environment, in other words, an expansion of what has been called external physiology, which might bear the newer title of ecology. But the wide-spread ignorance regarding the broad scope of physiology is in part explained by the fact that a large number of professed physiologists do busy themselves with, and most academic courses deal largely with, the vital phenomena of the internal parts of higher animals with the image of man ever in the background. The chief cause of this condition in turn is doubtless the rise of the science within

medical schools and its continued close association with them, as a result of which the attention of investigators and teachers has been necessarily focused largely upon internal problems. This aspect of the science is mirrored in the text books, and is the chief aspect that is presented to the youth in his early studies. Unfortunately the university student has only a limited opportunity to correct his early false impressions, for the university has not yet accorded to physiology its rightful heritage as a pure science. Its freedom in research can not be denied it, however, and popular misconceptions regarding its scope will disappear with its advance. The living of the living thing is the criterion by which the physiological phenomenon may be recognized.

The ways in which the vital process manifests itself seem at first sight numberless and incapable of mutual comparison. The contraction of a muscle, the secretion of a glandular product, the production of a sensation, the growth of an organism, the orientation of a motile body to rays of light, the passage of a nervous impulse, respiration, the circulation of blood, the transmission of a quality from parent to offspring, instinct, fatigue, a volitional act, the course of a germ disease, sleep, speech, laughter, thought, the digestion of food, the maintenance of bodily temperature, the hearing of sound, sight, the recognition by touch of a familiar object, memory, emotions, the inhibition of an existing action, hypnosis—at first thought these phenomena appear to be of quite different kinds, each *sui generis* and incapable of comparison with the others. Have they common factors? Is it possible to unify them?

Through the ages various attempts have been made to do this. The appearance of the first of these attempts was nearly coincident with the culmination of Grecian culture. From that auspicious time down to the great Roman physician Galen, then across the long stretch of thirteen centuries, bridged by Galenic tradition, but barren of physiological discovery, to the rebirth of scien-

tific, together with other, learning, and well into the seventeenth century, the doctrine of the *pneuma,* or spirits, reigned supreme. This doctrine was often expressed in vague, uncertain terms, and in the hands of the Stoic philosophers, the Pneumatic physicians, the scientific men of Alexandria, Galen and minor writers, it was variously portrayed. The *pneuma* was believed to be an extremely subtile material agent entering the body with the breath, and was spoken of as "very subtle air," "very lively and pure flame," "fluid," "of the nature of light," "vapor," "something analogous to the spirits of wine," and so on. Each vital action was a manifestation of its activity. In the heart dwelt the vital spirits; in the brain the animal spirits. They flowed and ebbed through the veins and arteries, they coursed along the nerves, they permeated the tissues, and they bubbled and effervesced. Through them the body felt and moved, was nourished and warmed, grew and reproduced. It was a genial, comforting belief, nothing was more plausible; in its light vital actions seemed simple enough; and so for two thousand years the spirits danced merrily along.

But there were hard-headed thinkers in the seventeenth century. We may even imagine that the skilful experimenter, Harvey, the discoverer of the circulation of the blood, had his doubts. It is true that Descartes made free use of the spirits in his clever portrayal of the working of the organic machine, but there were others, believers in the machine, who contended that its *Deus* was not the *pneuma.* The spirit of mechanism was in the air. With the beginning of a rational physics, stimulated largely by the discoveries of Galileo and Newton, and a rational chemistry, freed from alchemy, there arose those two curious groups of Utopian theorizers, the iatro-physicists and the iatro-chemists, led, respectively, by Borelli and Sylvius. The one looked at the actions of the living being through the spectacles of the physicist, the other through those of the chemist; to the one vital actions

were physical phenomena, to the other, chemical phenomena. Their gaze was in the right direction, and each believed that he saw a great light. But like the whole world of science of their time, they knew too little of the true physics and chemistry, and their interpretations of organic processes, while containing a considerable modicum of truth, teemed with unwarranted hypothesis. It was not strange, therefore, that the iatro-movement was short-lived. Its influence, however, was not without value, for as the knowledge of physiological fact increased through experiment, and the world became accustomed to mechanical notions, the authority of the spirits became weakened, and gradually, very gradually, they ceased to be a factor in physiological reasoning. In popular speech, however, they persist even to our own day; for, as our moods change, we are in good spirits or bad spirits, full of spirit or lacking in spirit, high-spirited or low-spirited—phrases which stand as witnesses of a once powerful, but now discarded, physiological doctrine.

As the spirits became deposed, scientific thinkers, dissatisfied with the mechanism of the time, still groped for something to take their place. There were spontaneous uprisings of such agencies as Van Helmont's *archeus,* Stahl's *anima,* Boerhaave's *principium nervosum* and Hoffmann's ether. None of these long survived, and soon after the middle of the eighteenth century they were definitely replaced and the wide-spread desire for a unifying principle was for the time set at rest by the hypothesis of vital force. All physiologists had now come to realize that many of the chemical and physical phenomena of inorganic nature were to be observed also in living bodies. But they knew that the chemical composition of the latter differed from that of the former, and for the manufacture of the vital substance and for many of its actions they could find no parallel outside of living bodies. Most of them succumbed to the compelling power of their ignorance and acquiesced in the assumption that a peculiar principle resides in living

things, a vital force (or energy, as we would call it to-day), differing in nature from the forces (or forms of energy) that exist in non-living things. Johannes Müller presented the vitalistic conception clearly as follows:

> "Organic bodies consist of matters which present a peculiar combination of their component elements, a combination of three, four, or more to form one compound, which is observed only in organic bodies, and in them only during life. Organized bodies, moreover, are constituted of organs, . . . each . . . having a separate function; . . . and they not merely consist of these organs, but by virtue of an innate power, they form them within themselves. Life, therefore, is not simply the result of the harmony and reciprocal action of these parts; but is first manifested in a principle or imponderable matter, which is in action in the substance of the germ, enters into the composition of the matter of the germ, and imparts to organic combinations properties which cease at death."

By the same author life is characterized as "the manifestation of the organic or vital force." Again, "Organic bodies participate in the general properties of ponderable matter. The laws of mechanics, statics and hydraulics are also applicable to them." The application of these laws to them is, however, "limited," from the circumstance that the causes of motion most engaged in them are essentially vital in their nature." A few bold spirits, like Reil in Germany and Magendie in France, argued against such a conception, but they formed a small minority, and the physiology of the time became essentially vitalistic.

This state of affairs prevailed for barely a century. Soon after its beginning oxygen was discovered, and the modern chemistry was begun. A few decades more and the new physics was founded on the doctrine of the conservation of energy. These two discoveries with their momentous consequences were epoch-making for physiology. The events of the inorganic world were at last conceived by the human mind in a rational manner, and the application of such conceptions to vital processes was not delayed. The assumption of a specific vital force was seen to be unnecessary. Men began to talk of vital phenomena in terms of the new sciences, and physiology

began to be defined as the science of the physics and chemistry of living things. Such is the prevailing conception to-day.

Is the vital process more than physics and chemistry? Two facts stand out strongly in the physiology of the present day. One is the constant extension of physico-chemical principles into the explanations of hitherto mysterious functions; the other the seeming inadequacy of those principles to explain other functions. In their attitude toward this apparent inadequacy physiologists, while disavowing with almost entire unanimity their belief in the vital force of a century ago, may be said to be collected at present into two camps. By far the majority, while not denying the existence of puzzling problems, are yet possessed of an optimistic spirit and look forward with serenity to the unraveling of the mysteries of the organism, as the mysteries of the inorganic become more clear. They look at life, not as a distinct entity permeating and vitalizing a complex machine, but rather as the sum of the activities of that machine. In the opposite camp there are a few souls who, though they too have cast off the dross of the old conception, are rendered impatient and despondent by the occasional failure of present knowledge to explain, and they fly for refuge to a refined and essentially inexplicable vital residuum. They have succumbed to the inevitable reaction that follows rapid progress. But they are not vitalists, they say, at least not paleo-vitalists: they are neo-vitalists. Into the intricacies of neo-vitalistic views and into the shades of difference existing between them it is not opportune here to go, for they exert practically no influence on the physiology of the time. The hopeful investigator continues his endeavors, and with success, to interpret vital processes in accordance with physico-chemical laws. It seems to me that this is the most promising method. For less than one hundred years has it avowedly been in vogue, and these have been the years of most rapid advance. In this time many mysteries seemingly inex-

plicable have been clarified. It is futile to deny future rapid progress along the same lines, and the solving of problems that now defy the ingenuity of the experimenter. We confess our ignorance and our frequent failures, but we believe that we are on the right track. Physics and chemistry are not completed sciences. Their youth indeed is hardly passed. Their greatest achievements are probably yet to come. If what we know of physical mechanism to-day is not sufficient to insure us an understanding of the physiological machine, then let us look to what we shall learn to-morrow. Whatever the ultimate outcome, the solace of the vitalistic conception, it seems to me, should be resisted until we are prepared with full knowledge to maintain the final inefficacy of the physico-chemical mode of interpretation. If such a time ever arrives, it must necessarily be far in the future.

If the vital process be capable of a physico-chemical interpretation, it is at once understood that the methods of the physiologist must be the methods of physics and chemistry. And this is the case. In the physiological laboratory we employ the same methods that are used in the physical and the chemical laboratories, modified only in so far as is necessary to adapt them to the material employed for study and the specific problems to be solved. Specific physiological apparatus of precision in great variety has been devised, and specific methods of using it. But the apparatus and methods are physical and chemical in essence. The physiologist's material for study must necessarily be living material, except in so far as it is possible to deduce the vital phenomenon from the phenomena of non-vital substances—a procedure which, though often necessary, as is especially the case in much of the work of the chemical physiologist, is a procedure of limited value. In external and in much of internal physiology the living organism is used intact. With many problems of internal physiology, however, the method of vivisection must be employed—a method, which, notwithstanding the occasional charges of the un-

informed, does not in either its theory or its practise imply cruelty or inhumanity.

Physiology has long since passed the stage where unaided observation alone is of value, and has become preeminently an experimental science. It is the task of the experimenter to alter one or more of the conditions under which the phenomenon occurs, to observe its change, if such appears, and thus to throw light upon the nature of the phenomenon itself, its relation to both its original and its changed conditions, and its causes. Herein lies the enormous difficulty of physiological work. The vital process is of a complexity unapproached, much less equaled, in the inorganic world. Living substance is never exactly the same at two successive periods. It is ever in unstable equilibrium, the seat of constant change, of augmentations and depressions, of physical and chemical mutations, and of what we in our ignorance call spontaneous activities; and the conditions of its activities are manifold and often obscure and unsuspected. To maintain the majority of these conditions intact, while altering one or more, is a superhuman task, one that is approached, but probably never realized in its entirety. The physiologist is thus constantly baffled in his pursuit of the desired object, and must needs exercise unwonted patience in the face of not infrequent failure. His progress is slow and his results can only approximate the mathematical exactness of the experimenter who deals with stable non-living matter.

Since the time when physiology assumed its physicochemical aspect and entered upon its modern phase, what has been the trend of its research? Its energies were first directed chiefly to the study of the mechanical and other physical problems of the organs of vertebrate animals. The electrical method of stimulating living substance was devised, by which the latter can be made to act at the will of the experimenter—a method the importance of which can scarcely be overestimated. The graphic method was early introduced and has been de-

veloped to the greatest refinement. By its use organic movements can be recorded graphically, and can then be easily analyzed into their space and time components and be studied at leisure. The working of the organs of the mammalian body, considered as physical machines, is now fairly well understood, although specific problems within this field are still being actively investigated. Very exact computations have been made of the amount of energy given off by the body in the form of heat and of muscular work, and it has been found to correspond very closely with the income of energy derived from the food and whatever bodily material may be consumed during the experiment. The principle of the conservation of energy applies as well to the living as to the non-living machine.

Chemical physiology, or, as it is now often called, biochemistry, developed gradually during the last century but did not become prominent until the last decade. It occupies now a foremost place among the branches of biological science. Much biochemical work is morphological; the determination of the chemical constituents and structure of substance once living, from which inferences may be drawn as to the chemical nature of living substance. Unfortunately, living substance can not be chemically analyzed directly, since all known methods at once kill it, and there is left only the non-living proteins, carbohydrates, fats and other organic and inorganic compounds, the individual bricks, or, better, cleavage products of the complex unity. In determining these and their relationships great progress has been made, but we of the present are far removed from that state of smug satisfaction of some of the earlier investigators, to whom a living body represented only so many molecules of carbon, oxygen, nitrogen, hydrogen, sulphur and phosphorus. The problems of the chemical physiologist, as distinguished from the chemical morphologist, are in general the problems of metabolism,—which the Germans have aptly styled "*Stoffwechsel*"—the chemical changes

undergone by matter in the process of living, its building up and its breaking down, its anabolism and its katabolism. The intricacies of metabolism can scarcely be conceived by one not familiar with the attempts to follow them, and the biochemists deserve much credit for the ingenuity of their methods. They have been most successful in determining and isolating the multitudinous katabolic products of vital activity, both the intermediate and the final products, and in discovering clues to the individual steps in the katabolic process. They have even succeeded in making synthetically many of these vital products, an achievement which was inaugurated by Wöhler in 1828 in the manufacture of urea. The laboratory synthesis of vital products has become, indeed, almost a daily occurrence and has hence lost its former miraculous appearance. It is not, however, certain that the laboratory methods and the physiological methods employed in such synthesis are identical. The steps of the anabolic process are still obscure, and until they are better known we can hardly look forward with confident satisfaction to the artificial manufacture of living substance. Yet physiological alchemists do exist, and the successful making of "life" has been heralded more than once to a sensation-loving world. Such an achievement is for the present only an idle dream, serving to gently and pleasurably titillate the cerebral cells of the dreamers.

Of recent years physiological physics and physiological chemistry have come to meet on common ground within the realm of the new science of physical chemistry. It has come to be clearly recognized that living substance consists of organic colloidal, or jelly-like, material, permeated by inorganic matter. The colloidal matter seems to consist of enormous complex molecules and aggregates of molecules; the inorganic matter partly of small, simpler molecules, and partly of ions, which are atoms or groups of atoms charged electrically. As the life process goes on, the living substance being now in a state of

activity, now in a state of rest, there is a constant chemical and physical interplay between the two material constituents, and a constant interchange between them and the surrounding medium, in which the laws of osmosis play a prominent part. The careful investigation of the nature of these internal and external exchanges seems to be illuminating many time-honored physiological enigmas, such as absorption, secretion, excretion and other instances of the passage of substances through membranes, the electrical phenomena of tissues, the nature of the nerve impulse, the fertilization of the ovum, and the general nature of chemical changes within protoplasm—enigmas which have been constantly quoted in support of the vitalistic conception. But we should not be tempted by success along these lines to claim, as is sometimes done, that the life process is merely ionic or electrical or osmotic in nature. In investigating physiological problems by the aid of modern physical chemistry, we seem to be brought at times periously near the electron theory of matter, and we are tempted to hazard the guess that the establishment of that theory would place the physiologist under renewed obligations to the physicist.

The study of ferments, too, is assisting—strange, innumerable, intangible bodies of uncertain nature, which, present in minute, almost imperceptible, quantities, seem to facilitate vital chemical actions without entering directly into them. In the early years ferments were recognized as mediating the processes of digestion, and but few of them were known. Of late their number has been enormously increased, and a corresponding number of intracellular or extracellular chemical processes has been ascribed to their action. Each has its own specific chemical reaction to facilitate, and, in many cases at least, their action is reversible, *i. e.*, one and the same ferment can aid both the decomposition of a complex substance into its constituents and the synthesis of those constituents into the complex substance. The ferments that function in vital processes are products of living matter,

but recent research makes it increasingly clear that they act merely like catalytic agents of inorganic origin. The study of ferments has its dangerous aspect, for more than one investigator, with an eye single to their universality and efficacy, has in his cyclopean enthusiasm come to suspect that all the chemical processes of living organisms are mediated by them, and has even been led to make the narrow and unwarranted assertion that life itself is merely ferment action.

The discovery of protoplasm and the establishment of the cell theory have exercised a profound influence on the science of function. Until nearly the middle of the last century physiologists were in a sense groping in the dark, for the reason that although they were endeavoring to unravel the mystery of living substance, they had no conception of the real nature of that substance. When the times were ripe they were quick to recognize the value and significance of the new discoveries, and, indeed, played valuable parts in formulating and establishing the new doctrines. With the clear recognition of a definite substance as the physical basis of life, their energies were more definitely directed than before. One result of this has been the increasing and powerful growth, during the latter part of the last century and the early years of this, of general physiology. The rise of general physiology represents a movement away from the earlier study of the mechanics of organs, toward that of the vital phenomena of living substance itself, irrespective of its special position within the organism. General physiology is preeminently the physiology of to-day, whether its point of view and methods be physical or chemical.

The principle of organic evolution is in its essence a physiological principle. It represents a great physiological experiment which nature has been making since the beginning of living things, and is continuing to make. But the discovery of the facts and principles of organic evolution and the establishment of its theory have been

accomplished only in small part by professed physiologists. Not even has the evolution of function—a field of great possibilities—been explored, except in a few small and isolated spots. The necessity of properly controlled experimentation in settling the vexed problems of evolution is, however, at last being recognized, and the next few decades promise to witness great advances in the discovery of the ways in which nature has made her great experiment.

It is not strange that with its intricacies and peculiar difficulties the solving of the problems of nervous function has proceeded slowly. The facts that nervous function is a property of the nerves, and that the brain is the seat of the mind were probably first capable of scientific proof by the Alexandrians in the fourth century before Christ. The two great functions of sensation and motion were also recognized by the ancients, but that they were mediated by different nerves was first demonstrated by Sir Charles Bell, so late as 1811. The idea of the specific energy of nerves—a phrase which means specific activity—or the general principle that each nerve has specific functions with which it always responds, no matter how stimulated, was definitely proposed by Johannes Müller in 1826 for the nerves of special sense, and later was generalized for other nerves and other tissues. Since then great progress has been made in discovering by experiment the specific functions of individual nerves and in formulating therefrom theories of the general functions of nervous tissues. That different nervous activities are associated with different portions of the brain was early surmised, and before the middle of the past century such important nervous centers as those controlling respiration and the beat of the heart became located. Since then the nervous mechanism of a host of unconscious organic processes has been discovered. That the psychic portion of the brain does not function as a unit, but consists rather of a complex group of nervous organs, each with its specific functions—a fact

that is of great moment in elucidating the relations of brain and mind—has been known for only a little more than thirty-five years. For it was in 1871 that Fritsch and Hitzig, by stimulating specific small areas of the surface of the cerebrum and obtaining in response specific muscular movements, first demonstrated a specific cerebral localization of functions. Since then the task of mapping out the outer layer, or cortex, of the cerebrum of a few mammals and man into centers, joined by nerve fibers with specific organs of the body and employed for the control of separate groups of muscles and for the work of the special senses, has proceeded to a considerable degree. Thus, we are now able to point to a certain portion of one of the convolutions of the cerebrum and say that its nerve cells, or neurones, mediate the volitional act of contracting one's biceps muscle; we can say that the neurones in other localities mediate the separate acts involved in locomotion; in others, the changes of facial expression; and in still others, the enunciation of thoughts in the form of spoken words. We know with considerable exactness the positions of the separate centers for sight and hearing; less exactly those of the other special senses. Besides the sensory and motor centers, evidence points strongly toward the existence also of cortical regions which are elaborately joined to one another and to the sensory and motor regions by means of innumerable nerve fibers, and the function of which is to correlate, harmonize or associate the work of the sensory and motor centers. Such association centers thus help to mediate the more complex psychical phenomena, such as memory and the association of ideas. We can even formulate helpful hypotheses of the neural accompaniments of various psychoses. According to James's theory of the emotions, for example, the perception of the automobile about to run us down leads to the feeling of fear only through the mediation of various organic processes, such as a quickening of the heart beat, pallor and trembling. The accompanying series of

neural processes would consist in the activity, in turn, of visual sense organs, neurones conveying the visual impressions to the brain, cerebral neurones mediating the sensation and perception of the terrifying car, motor neurones controlling the peripheral muscular actions that are involved in the organic processes, neurones conveying to the brain the impressions of altered heart beat, constricted arteries and trembling muscles, and lastly cerebral neurones mediating the feeling of fear. Because of its difficulty, much of the work of geographical exploration within the central nervous system is at present necessarily inexact, and moreover there is still much *terra incognita*. And even though we have thus come to know the gross functions of specific parts of the higher mammalian and human brains, we still know all too little of the processes by which the different parts are coordinated and made to subserve the many complex needs of the organism. The recent work of Professor Sherrington on the integrative action of the nervous system is an admirable example of the kind of investigation that is needed in this field, and by its very excellence helps to emphasize the lack of our knowledge. The laboratories of physiological psychology, now numerous, are making many valuable contributions, especially to our knowledge of the mechanism of the special senses. But when I make a summary of what we now know of the physiology of the nervous system, I come to realize anew its paucity, compared with what we ought to know and shall know, I am confident, in the long future. Here, it seems to me, is a field sadly needing tillage, and one where, though tillage be extremely difficult, the yield is certain to be rich.

All investigation here will lead up, in a sense, to the solving of that problem of problems, which has been for ages the focus of discussion and speculation, the problem of consciousness—"at once the oldest problem of philosophy and one of the youngest problems of science." For centuries it has been thought about, talked about, written about, and with what result? The elaboration of

hypothesis after hypothesis, which smell of the lamp—fabrications of the philosopher's cell rather than of the physiologist's laboratory. Almost without exception they are elaborate exercises in dialectics, rather than real portrayals of the nature of that most striking of physiological phenomena. To the physiologist they are almost without exception arid and unsatisfying. "Words, words, words," replies Hamlet to the question of Polonius. At first thought, the theories of dualism and interaction seem best adapted to the obvious facts of human experience: the brain and mind are two distinct entities usually intimately associated, and each capable of inducing phenomena in the other. But deeper brooding, and especially a recognition of the mode of action of the non-psychic portions of the nervous system and the close dependence of psychic on cerebral phenomena, of "how at the mercy of bodily happenings our spirit is," make us seek a more genuinely physiological explanation.

The physiologist recognizes as the morphological basis of nervous actions the neurone or nerve cell, consisting of a compact cell body, from which radiate outward filaments, the nerve fibers. He finds in the nervous system of the higher animal or man millions of such neurones and many more millions of nerve fibers. These constitute seemingly a confused and inextricable mass, but by careful study he has been able to discover an exact and definite, though excessively intricate, nervous architecture. He finds that the bodies of neurones act as central stations, to which and from which flow the nervous impulses along the nerve fibers: the incoming impulses constituting the centripetal, or afferent, or sometimes sensory, impulses; the outgoing constituting the centrifugal, or efferent, or sometimes motor impulses. He recognizes as the physiological basis of nervous action, the reflex action, consisting of an afferent impulse, a central process, and an efferent impulse. He sees reflex acts combined in innumerable ways, and augmented and depressed by other reflex acts. He sees many of the most

complicated actions of the individual performed with the aid of this reflex mechanism and without the aid of consciousness. He recognizes that a large proportion, if not the majority, of the individual's actions are reflex and unconscious actions. Lastly, he finds in reflex mechanisms no mysterious principle, but an ensemble of the same physico-chemical phenomena, which in one form or another he finds in other than nervous tissues, and in which the principle of the conservation of energy holds good. Turning now to conscious actions, he sees how indispensable to them, at least in the higher animal species and man, is a certain part of the cerebrum, especially the outer layer or cortex; and how the degree of intellectual development varies with the extent and complexity of this material structure. He sees how injury or disease of this part, or anything interfering with its proper activity, changes the individual from a sentient being into a non-thinking reflex machine. He sees acts, once consciously performed, now relegated to the unconscious reflex sphere. He sees how consciousness disappears in sleep, and how its manifestations vary under the influence of drugs. The cerebral cortex is composed of numberless neurones and is connected by afferent and efferent paths with the other portions of the nervous system. With these facts in mind, and though recognizing the intricacies of mental phenomena, the physiologist gets into the way of thinking that after all the mechanism of cortical actions is really the same as that of other nervous phenomena. He sees no objective, *a priori* reason why an entirely new causative principle should be introduced to explain the action of this small fraction of the nervous system. Whatever its nature, consciousness appears to him, not as a distinct entity grafted on to certain nerve structures, but as merely one of the modes of manifestation of the activity of those structures, just as chemical, thermal and electrical phenomena are other modes. Being thus one of the signs of nervous activity, the physiologist finds it difficult

to see how consciousness can act as a cause of nervous activity, any more than can the heat given off in such activity react to produce itself. The physiologist sees that nervous systems, with all their functions, have undergone an evolution; he recognizes orders of consciousness—a low, simple, gradual beginning, he knows not where, a progressive increase in complexity as nervous systems complicate, and the final culmination in self-conscious man. The relations of consciousness in its simplest form to the nervous system seem to be the same in kind as in the human being. For the physiologist, looking at the matter in this light, Huxley has probably formulated the best working hypothesis in his famous essay, "On the Hypothesis that Animals are Automata." After a lucid analysis of the actions of animals lower than man, he says:

"The consciousness of brutes would appear to be related to the mechanism of their body simply as a collateral product of its working, and to be as completely without any power of modifying that working as the steam whistle which accompanies the work of a locomotive engine is without influence upon its machinery. Their volition, if they have any, is an emotion indicative of physical changes, not a cause of such changes."

And later:

"It is quite true that, to the best of my judgment, the argumentation which applies to brutes holds equally good of men; and therefore that all states of consciousness in us, as in them, are immediately caused by molecular changes of the brain substance. It seems to me that in men, as in brutes, there is no proof that any state of consciousness is the cause of change in the motion of the matter of the organism. If these positions are well based, it follows that our mental conditions are simply the symbols in consciousness of the changes which take place automatically in the organism; and that, to take an extreme illustration, the feeling we call volition is not the cause of a voluntary act, but the symbol of that state of the brain which is the immediate cause of that act. We are conscious automata."

Objection after objection has been raised to the automaton hypothesis. It has been dialectically disproved many times. Its upholders have been charged with all the sins against logic, common sense, lucubration, spirituality and orthodoxy. And yet it will not down, for of all hypotheses it seems to accord most closely with the facts

of neural physiology, as we know them to-day. It may perhaps prove to be not a finality; but whether in the distant future it be found correct or incorrect, it is from its general standpoint, it seems to me, that the physiologist of the present epoch can do his most helpful experimental work. The problem of consciousness should be taken into the physiological laboratory, and the conditions of the manifestation of psychic phenomena should be investigated by laboratory methods. All mental processes, even to the last degree, are dependent on and have their basis in brain processes. The physiologist should study in minute detail the cerebral process of each mental act. He can thus inform the psychologist as to the conditions under which psychic phenomena occur. "An individual fact is said to be explained," says John Stuart Mill, "by pointing out its cause." And again, "The cause of a phenomenon is the assemblage of its conditions." In this sense the explanation of consciousness, it would appear, ought to come, sooner or later, from the physiologists.

I have spoken of the physiological aspect of other sciences. Pathology, the science of disease, or, in other words, perturbed function, is peculiarly close to physiology, for there is no sharp line of demarcation between the normal and the abnormal. We may assume the successive chemical substances involved in a certain progressive physiological act to be represented by the series *A, B, C, D,* in which *A* is the substance from which the chain proceeds. By analytic and synthetic processes *A* gives rise to *B, B* to *C* and *C* to *D,* which is the final end-product of the metabolism. Even with the same quantity of *A* and the same strength of stimulus, the quantities of *B, C* and *D* produced in successive repetitions of the act may vary considerably, owing to unknown factors. It is only when the intermediate or final products become markedly increased or diminished in quantity in comparison with their usual amounts, that we speak of the function as pathological. The excitability of cells may be greatly augmented or diminished and still be within the

limits of the normal. A tissue may grow excessively, as in tumors, or may waste away, and yet normal function be not seriously interfered with until remote limits are passed. Bacteria may live physiologically within an animal body. They produce and cast off toxins, which intrinsically are poisonous to the cells of their host. These, however, cause a physiological production of antitoxins in the body cells. So long as the antitoxins are sufficient in quantity and strength, they neutralize the poisonous toxins. If the latter get the upper hand they augment or depress the physiological activities of the cells of the host, and we speak of the result as a perturbation of function. The power of the organism to adapt itself to changed conditions and to maintain its physiological status is little short of marvelous. When, in spite of all endeavors, the physiological status is overwhelmed, then is the time for the pathologist to investigate and the physician or the surgeon to attempt to cure.

As in the biological sciences, so in the medical art, there exists a distinction between the morphologist and the physiologist, between the surgeon and the physician. The surgeon is the medical morphologist. His task is to remove diseased or injured tissue, to reunite separated structures, to restore structure or stimulate to its restoration, in short, to make structure normal, so that normal function may follow. The physician, on the other hand, is the medical physiologist. It is his endeavor to restore normal function. His life-long labor is an exercise in physiology. He should know his physiology as the surgeon should know his anatomy, minutely and to the last degree. He should know what health is before he tries to restore it. We all realize how rarely this ideal is reached, and we all have experienced the dire results of medical empiricism. Huxley likens nature and disease to two men fighting, the doctor to a blind man with a club who jumps into the mêlée, and strikes out right and left, sometimes hitting disease and sometimes hitting nature. Would not his blows be more telling if he were quite sure which of the combatants were nature and which

disease? Wherein he fails to avail himself of present knowledge he is culpable. And yet he is not to be charged with the whole burden of his failure to cure. Some of this should be shared, I regret to confess, by the physiologists, for they still know too little of the normal action of the vital mechanism. So far is this true, that I am convinced that one of the surest and quickest means of inaugurating a rational and effective art of medicine is through the advancement of physiological discovery. All physicians must be in part empirics until the physiological millennium is ushered in.

If I have been understood aright, my hearers will have perceived that with a mighty subject matter which is preeminently its own, physiology extends a leavening influence into a host of other sciences and medicine as well. It is an unusually good example of the typical pure science, with its outlying affiliations and applications. Like many another natural science, its rise, growth and early nurture were under the protecting wing of medicine. The physiologists of the early years, when their science was crystallizing out of the common mass of scientific knowledge, the men who first formulated its principles, and they who in later years developed it, were, with few exceptions, men of medical training who were under the influence of medical traditions and were guided by the medical spirit. In recent years the ties of the old traditions have been loosened, and the science is passing out from the parental shelter into the illimitable atmosphere of scientific freedom. Its aspirations in research are unhampered. Its achievements in research, in so far as it constitutes an academic theme, are limited by the fact that, except in a few isolated cases, physiology is still regarded by the university as primarily a medical science and its laboratories are housed in medical schools. This is a relic of early history. In consequence physiology must constantly breathe the medical atmosphere and must be influenced, whether it will or no, by medical ideals. This is not to be deprecated from the standpoint of physiological medicine, and the reciprocal advantage

to physiology itself in this one aspect is also great. But this now anomalous state of affairs leads directly to two consequences: namely, first, that the broader biological aspects of the science are less dwelt upon than otherwise would be possible; and secondly, that where such aspects have been investigated the work has been done largely by men not professed physiologists and usually lacking the latter's exact training as experimentalists. The customary academic position of the science thus imposes a certain restraint upon physiological progress, and delays its full fruition.

It is idle to try to predict the ultimate fate of the science that is attempting to make clear the vital process. To some minds it is attractive to speculate, and even to dogmatize, concerning the limits of natural knowledge. The present task of the physiologist is to investigate, and continue to investigate, ceaselessly and fearlessly, with a spirit ever fresh and hopeful, seeking only the elusive truth, unmindful of the limits of natural knowledge and undeterred by the fear that the mystery of life will ever remain a mystery. He must be content to spend his energies in patient laboratory research, accumulating facts, unifying facts and deducing laws for limited spheres of vital activity, and thus to lay the foundations for the broader generalizations that will come after his labor has ceased. By his constant association with the material substratum of the life process and the continual discovery of new and undreamed-of possibilities in its action, he gains a respect and even reverence for living matter which only he can possess. None but he can realize and understand its supreme beauty and harmony and sublimity. He can not sympathize with, much less share, the feeling that the material is base and only the spirit is uplifting, for to him the material makes its uplifting nobility manifest. He likes to believe, and to act on the belief, that no physiological problem is forever insoluble, and though ignorance may be long-lived, he sees no necessary reason for an ultimate, eternal *ignorabimus*.

NOTES AND LITERATURE

BIOMETRICS

Recent Contributions to Theory.—For obviously necessary reasons biometric work in the past has fallen, and for a considerable time in the future will continue to fall into two sharply separated categories. The first of these is the development of mathematico-statistical methods for dealing with biological material. The second is the concrete application of these methods to biological problems. Developments of higher mathematical theory will never be in and for themselves of particular interest to the great majority of biologists. Their only interest to the biologist exists in what they are practically good for; if there is developed any new mode of thinking or of investigation which will help to solve a problem it is of importance to know about it so that use may be made of it. The same consideration applies in regard to the applications of biometrical theory. To the biologist who is not cultivating this particular field of research the results obtained in it will be of interest only in so far as they appear to make significant contributions, expressible in terms intelligible to any non-mathematically trained person, to the solution of significant problems. There can be no doubt that valuable contributions to biology are being made by workers in biometry. Further, it is believed that this fact would be more generally recognized than is now the case, were the methods and results stated in a terminology less strange and repellent to the average biologist than is the mathematical. In accordance with this belief it will be the aim of these notes to set forth as clearly as may be and in a non-technical way the significant advances in biometrical research. Recent contributions to biometric theory will be considered in the present note. Work in the direction of the application of biometric methods to the solution of concrete biological problems will be discussed in subsequent notes.

The degree of trustworthiness of any reasoning from statistical constants of whatever sort must ultimately depend upon the values of the "probable errors" of these constants. The probable error is a measure of the limits of accuracy of the constant to which it applies. A number of recent papers deal

with various points regarding the general theory of probable errors. W. F. Sheppard, in a paper giving the mathematical proof of his corrections for the moments of frequency distributions,[1] points out that theoretically the raw value of the second moment rather than the value obtained by applying his corrections should always be used in calculating the probable errors of the mean and standard deviation. The present writer[2] shows by the consideration of concrete examples that the point made by Sheppard is not likely ever to be of any *practical* significance to the working biometrician. It makes no sensible difference in the actual result whether one does or does not use the corrected value of the second moment in determining these probable errors. In the same paper it is shown that a very considerable error may be made by using the formula ordinarily given for the probable error of the standard deviation when the distribution of variation differs considerably from the normal curve in certain particulars. One must always be cautious in assuming that a deviation from normality will be of no consequence in calculating probable errors.

A novel and important point regarding the probable error of a mean has been thoroughly investigated and solved by that mysterious person "Student,"[3] who has previously contributed to the pages of *Biometrika* under the same *nom de plume*. In passing it may be remarked that the propriety of publishing serious contributions to science under an assumed name seems questionable; one had supposed that those conditions no longer existed which in earlier times made such a course not merely desirable, but often indeed necessary if the same individual were to continue to contribute to science. To return to the point. In all kinds of experimental science the following type of problem very frequently arises; a series of say 10 or fewer experiments are tried under certain experimental conditions which may be denoted by the letters $a, b, c, d, \ldots n$. A second series of equal extent is then tried with, say, one experimental condition changed so that the conditions are now $q, b, c, d, \ldots n$. With what degree of probability may it be asserted that an observed differ-

[1] Sheppard, W. F. The Calculation of the Moments of a Frequency Distribution. *Biometrika*, Vol. V, pp. 450–459, 1907.

[2] Pearl, R. On Certain Points concerning the Probable Error of the Standard Deviation. *Ibid.*, Vol. VI, pp. 112–117, 1908.

[3] "Student." The Probable Error of a Mean. *Ibid.*, Vol. VI, pp. 1–25, 1908.

ence in the results of the parallel sets of experiments is *real*, that is, is due to the changing of condition a to q and not merely a chance result of random sampling? On account of the statistical smallness of such experimental series, coupled with the fact that the results usually deviate widely from the normal distribution of errors, the usual theory of the probable error of a class frequency or of a mean fails to give an adequate answer to the problem. "Student" has done the great service of providing formulas to cover the case. He furthermore gives a table of probabilities for series involving four to ten experiments, inclusive, wherefrom the answer to such a question as that propounded above may be read off at once when the experimental data are at hand. In the original paper concrete illustrations of the use of the table are given, based on published experimental data in the fields of physiology and of agriculture. No particular mathematical knowledge or skill is necessary to use this table and its importance to the experimental worker is obvious.

On this same topic of probable error Pearson and Lee[4] have recently made an important contribution. While the investigation itself is of a complex mathematical character, the essential point is this: Suppose a number of bodily characters (say six to eight) to be measured in a large sample of a population. There are likely to be a very few individuals out of the whole sample that differ rather widely from all the other individuals. What is the probability that such outlying individuals do not really (*i. e.*, biologically or genetically) belong to the population from which the sample is drawn, but only happen to get into the sample by accident? The solution to this problem is what Pearson and Lee attempt to give.

Along with these investigations on probable errors is to be included a recent paper of Pearson's[5] on the relation of past experience to future expectation. The nature of the problem discussed may be indicated by an example. Suppose that a sample of 100 individuals out of a population be examined and 2 per cent. of these individuals be found to be suffering from some particular disease. What percentage of a second sample of 100 may reasonably be expected to show the disease? The

[4] Pearson, K., and Lee, A. On the Generalized Probable Error in Multiple Normal Correlation. *Ibid.*, Vol. VI, pp. 59–68, 1908.

[5] Pearson, K. On the Influence of Past Experience on Future Expectation. *Phil. Mag.*, 1907, pp. 365–378.

answer usually given is that 2 per cent. is to be expected, with a probable error of a certain amount. In calculating this probable error in the ordinary way it is assumed that the distribution of chances is given by the normal or Gaussian curve of errors. Pearson shows that this is not true except (1) when the first sample is indefinitely large in proportion to the second, and (2) when the characteristic does not occur in either a very large or very small percentage of the population. He then proceeds to develop general formulæ from which one may determine first the average expectancy for the second sample and its true probable error, and second the frequency of future samples having varying degrees of the characteristic under consideration. These methods are fully illustrated with numerical examples. The usefulness of the methods for biological work may be indicated by an example. Suppose that in a sample of 200 tadpoles, 106 are males and 94 females. Suppose, further, that in a second sample of 300 collected later in the season the proportion is 171 males to 129 females. Is it to be concluded that between the collections some factor has come into operation tending to the greater production of males? Or, on the other hand, is the proportion exhibited in the second sample what might be regarded as a reasonable chance deviation due to random sampling in a population wherein the sex, determining factors had not changed since the first sample was collected? The paper under discussion furnishes the methods whereby questions of this sort may be definitely answered.

Another recent contribution of Pearson's[6] furnishes new methods of determining the degree of correlation between variates. The methods are adapted for use in cases where for one reason or another it is not feasible to use the ordinary product-moment method of finding a correlation coefficient. It is neither possible nor desirable to enter upon any detailed discussion of the mathematical features of these new methods here. Three new methods are given. The first, or "difference method" of determining correlation, furnishes a very simple and tolerably accurate way of deducing a correlation coefficient from a symmetrical (*e. g.*, homotypic) correlation table. The other two methods are con-

[6] Pearson, K. Mathematical Contributions to the Theory of Evolution —XVI. On Further Methods of Determining Correlation.

Draper's Company Research Memoirs. Biometric Series, IV, pp. 39, 1907. (London: Dulau & Co.)

cerned with the problem of determining correlation from material arranged in ranks. The most obviously simple way of dealing with any mass of statistical material is to arrange the individuals in a long row in order of ascending magnitude of some character. It is not even necessary that the character be accurately measurable on a quantitative scale to make such a row. The second, and on the whole most important of Pearson's new methods, shows how to deduce true variate correlation from the correlation of ranks. The method is less accurate than the usual product moment method. The third method deals with the determination of variate correlation from the positive difference of ranks. Regarding these last two methods Pearson's general conclusion is "that variate correlations found by ranks may prove to be a useful *auxiliary* method of dealing with correlation, when it is needful to give a rough answer to a problem in a brief time, or when the material itself is incapable of being accurately measured."

In connection with this matter of the analysis of statistics by the method of ranks or grades it is of interest to note that Galton has recently published a table[7] of deviates of the normal curve which will be found useful in practical statistical work. In the text accompanying the table (which is calculated by W. F. Sheppard) the use of the method of grades in dealing with material not susceptible of exact numerical measurement is discussed.

Of value for practical biometrical computing work is an editorial note[8] in the current number of *Biometrika* giving an easily calculated and extremely exact formula for the Γ function. This function is frequently used in statistical work, particularly in curve fitting.

RAYMOND PEARL.

PROTOZOA

Some Amœba Studies.—The amœboid organisms include a vast number of minute bits of glairy protoplasm which live in widely different places sometimes free in ponds and pools, sometimes confined as parasites, to the narrow limits of a single tissue. To

[7] Galton, F. Grades and Deviates. *Biometrika*, Vol. V, pp. 440–406, 1907.

[8] On a Formula for Determining $\Gamma(x + 1)$. *Ibid.*, Vol. VI, pp. 118–119, 1908.

group all of these living things under the one generic name of Amœba is to confess the weakness and artificiality of classification. Schaudinn[1] attempted to bring some order into the group by adopting Cassagrandi and Barbagallo's generic name Entamœba to cover the ordinary parasitic forms of the digestive tract. These differ from the common *Amœba proteus* quite as markedly as do other genera of rhizopods, and whether they differ generically among themselves is a matter to be decided only when the life histories are made out.

Notwithstanding the hundreds of observations that are annually made on these amœboid organisms, there has been very little consecutive work on the changes of the protoplasm from beginning to end of the life cycle. Indeed, biologists would have extreme difficulty in picking up the thread of such a life history at either end, for observations and descriptions of conjugation or fertilization are most contradictory and confusing. The confusion will probably straighten out as soon as it is recognized that the varied accounts undoubtedly refer to quite different species or even genera of organisms. Schaudinn's description (*op. cit.*) of the process of fertilization in *Entamœba coli* was peculiarly daring, for autogamy amongst the unicellular animals was then a rare phenomenon, known to occur for a certainty only in Actinosphærium. Some such unusual process might be anticipated, however, in view of the fact that despite the thousands of eyes that annually study the amœboid forms, none have witnessed an ordinary form of conjugation amongst them. Schaudinn's excellent work on *Entamœba coli,* safeguarded by long experience with different kinds of protozoa study, and controlled by parallel studies on free-living rhizopods of other types must not be lightly brushed aside as too bizarre for serious consideration, especially as it has been confirmed in every detail by Wenyon[2] upon *Entamœba* (*Amœba*) *muris,* an intestinal parasite of the mouse.

According to Schaudinn, the cell of *Entamœba coli,* when mature, throws out all foreign matter and waste matter of its own metabolism, becomes more compact, smaller and spherical, and secretes a thick slightly refractive gelatinous membrane. The nucleus then divides by a primitive type of

[1] F. Schaudinn. Untersuch. über d. Fortpflanzung d. Rhizopoden. Arb. a. d. Kais. Ges.-Amt., XIX, 3, 1903.

[2] C. M. Wenyon. Observations on the Protozoa in the Intestine of Mice. *A. f. Prot.,* Supp. 1, Festband R. Hertwig, 1907.

mitosis into two nuclei which are separated from one another by the entire diameter of the cell. The nuclei then fragment, forming chromidia, while the cell becomes incompletely divided into daughter cells. In some cases the entire nucleus of each half disappears in the mass of chromidia granules; in other cases there appears to be a secretion of the chromidial substance as in Arcella, but in all cases a portion of the nuclear material is thrown out of the nucleus to degenerate. From the chromidia granules a new and smaller nucleus is formed in each half of the cell. Each then divides by a primitive mitosis into two nuclei, one of which degenerates, the other divides a second time and again one of the resulting daughter nuclei degenerates. After this process, which Schaudinn interprets as the equivalent of reduction and polar body formation in metazoa, the final encystment takes place. The gelatinous membrane disappears and in its place a much more refractive cyst membrane is secreted. The contents of the cyst become closely united again and the two remaining nuclei are brought together. Then follows a third division by mitosis characterized by long connecting strands which lie parallel with one another in the center of the cell and so that the daughter nuclei lie side by side in pairs. These paired nuclei then fuse, an eighth part of one of the original nuclei uniting with an eighth part of the other. Each cyst thus contains two fertilized nuclei, each of which subsequently divides twice to form eight nuclei. In this condition the cyst passes into the intestine of a new host, where the protoplasm divides into eight spores each with one nucleus. Wenyon's account of *Entamœba muris* confirms Schaudinn's in all essential features.

While *Amœba proteus* is probably far removed, phylogenetically, from Entamœba, there is reason to believe that the processes of fertilization have something in common. Four years ago Calkins[3] found what he regarded as evidences of a sexual phase in the life history, and described the multiplication of primary nuclei and the fragmentation of these nuclei into chromidia. The chromidia were interpreted as the possible nuclei of future gametes, an interpretation in line with the processes and outcome of chromidia formation in Foraminifera, in Arcella, Centropyxis, Difflugia and other rhizopods. Subse-

[3] G. N. Calkins. Evidences of Sexual Cycle in the Life History of *Amœba proteus*. *A. f. Protist.*, V, 1904.

quent observers, overlooking the fact that the stages in question must be very rare, have taken the ground, for the most part, that the evidence presented was too fragmentary to justify the conclusions reached. Some, like Schubotz,[4] while admitting the chromidia, claim that the organism is not *Amœba proteus*, and that the chromidia are not evidence of a sexual cycle; others like Prandtl,[5] forgetting that the cells under discussion were in a period of unusual physiological activity, attempted to explain them as pathological specimens with degenerating nuclei; and still others considered the scattered chromidia as possible parasites. The latter point of view was maintained by Prandtl[6] in a publication subsequent to the one just mentioned and in which the history of an Amœba-infesting parasite was made out. In this paper he hazarded the guess that the so-called multinucleate stage of *Amœba proteus* was in reality an ordinary form of Amœba infected with some species of Allogromia. This idea was undoubtedly suggested by the superficial resemblance between Prandtl's infected amœbæ and the photographs of the multinucleate *Amœba proteus*. Added experience would unquestionably have altered this conclusion, but the untimely death of this brilliant young investigator put an end to a career of great promise.

It was probably such experience that prompted Doflein to refrain from suggesting the possibility of an infection of *Amœba proteus* with some species of Dangeard's Nucleophaga. Doflein[7] found that the giant nucleus of *Amœba vespertilio* is a degeneration nucleus due to the presence of an intra-nuclear parasite *Nucleophaga amœbæa*, discovered by Dangeard in 1895, and he calls attention very properly to the possibility that many of the supposed chromidia in Amœba and allied forms may be parasites or stages of parasites of like nature. A similar parasite in the macronucleus of *Paramecium caudatum* was described by Calkins[8] as an intra-nuclear parasite similar to the intra-nuclear

[4] H. Schubotz. Beiträge zur Kenntnis der *A. blattæ* und *A. proteus*. *A. f. Protist.*, VI, 1905.

[5] H. Prandtl. Die physiologische Degeneration der *Amœba proteus*. *A. f. Protist.*, VIII, 1907.

[6] H. Prandtl. Der Entwicklungskreis von Allogromia sp. *A. f. Protist.*, IX, 1907.

[7] F. Doflein. Studien zur Naturgeschichte der Protozoen. V. Amöbenstudien. *A. f. Protist.*, Supp. 1, Festband R. Hertwig, 1907.

[8] G. N. Calkins. The Life History of *Cytoryctes variolæ* Guar. In Councilman's Studies on Variola. *Jour. Med. Research*, 1904.

phase of the smallpox organism. But between this parasite and the chromidia of *Amœba proteus* there is not the slightest trace of resemblance.

In the earlier paper it was supposed that the chromidia stage is only the antecedent of the later gamete formation and that conjugation of gametes is the method of fertilization. In a later paper Calkins[9] described some further studies made upon the same material after the amœbæ had been removed from the balsam, embedded in paraffine and sectioned. The supposed chromidia granules were then described as minute secondary nuclei which unite two by two, each couple giving rise to a reproductive body similar to a sporoblast. There were many gaps in this later account of fertilization and much remains to be done before the fertilization of *Amœba proteus* is established, but these later observations indicate a fundamental agreement with Schaudinn's description of fertilization in Entamœba. Chromidia formation seems to be an expression of some deeply lying biological activity concerned with the germ plasm and with fertilization. In some forms, as Arcella, Polystomella or Centropyxis, the nuclei of conjugating gametes are formed by the coalescence of such chromidia. In *Entamœba coli* there is a similar coalescence to form gametic nuclei, while fertilization is autogamous. In *Amœba proteus* the original nucleus of the cell divides repeatedly, the resulting nuclei break down into fragments, each of which is a complete gametic nucleus. Fertilization is again autogamous and chromidia formation s. str. absent.

It must not be forgotten in comparative studies of this kind that the organisms are widely different and that the expression of the fundamental biological activity underlying chromidia and fertilization is worked out in widely different ways. This obvious and trite observation has not been heeded in a recently published work on parasitic rhizopods by E. L. Walker.[10] Carried away, apparently, by success in raising amœboid organisms in large quantities by using artificial culture media recommended by Musgrave and Clegg, Walker has allowed to slip away a valuable opportunity to contribute something new to our knowledge of intestinal forms of rhizopods, while, on the other hand,

[9] G. N. Calkins. The Fertilization of *Amœba proteus*. *Biol. Bull.*, XIII, 1907.

[10] E. L. Walker. The parasitic Amœbæ of the Intestinal Tract of Man and other Animals. *Jour. Med. Research*, XVII, 1908.

he has allowed his imagination to lead him into generalizations involving totally different organisms. Here is one danger of the use of artificial culture methods in studying protozoa. The enormous numbers obtained tend to obscure the varying phases of vitality that characterize the life cycle of protozoa. The study of protozoa, even when it is possible to apply bacteriological methods, is fundamentally different from bacteria study. The latter dependent upon growth conditions, colony formation, reactions to media, etc., are essentially physiological. Protozoa study, on the other hand, is essentially morphological and is based upon the structures of the protozoan cell, involving all changes in cell structure which an individual (in the cyclical sense) undergoes during various phases of vitality. Hence it becomes necessary, first of all, to know the life history of a protozoon and the fundamental structures which its protoplasm assumes at different periods of vitality. Mere number of cells in any given phase is not satisfactory and here is where Walker falls into a trap. He fails to find stages described by Schaudinn and Wenyon, in his agar cultures and gives the inference at least that their observations were incorrect, all without taking the trouble to obtain his organisms in the corresponding stages of vitality. Schaudinn, in one set of observations to fill out the sexual phase of the life history, watched his material for weeks without finding the stages desired, and, to get them, finally swallowed the contents of a number of dishes, thus inoculating himself. His experiment was successful and he obtained what he wanted. This heroic method of procedure is not absolutely necessary, for abundant material may be obtained by inoculating lower animals; even such experiments, however, were not made apparently or, if made, not described by Walker. Such neglect vitiates all criticism or comment by the author, of conclusions of others regarding the sexual cycle of intestinal rhizopods and *a fortiori* of free-living *Amœba proteus,* an entirely different kind of organism.

Not even in regard to the ordinary vegetative phases of his organisms does Walker do justice to the material. The undoubted reproduction by budding is entirely overlooked; the term "spore" is misused throughout and the "extrusion" of fully formed reproductive bodies is very questionable. If such a method of endogenous bud-formation actually obtains, then, as an entirely new phenomenon in these rhizopods, it certainly

deserves more than the superficial description which the author gives. It is difficult to conceive how the budding process could have been overlooked, for in Entamœba under culture on agar, this process is apparently the most common method of reproduction. It is quite probable that development of the extruded so-called "spores" as described is the actual development of such buds. The finer details of structure were not made out, the origin of chromidia granules and their fate are not described, owing, possibly, as the author admits, to faulty technique (p. 418). Much dependence is placed upon the *cyst*, but there is no evidence to indicate that the author is cognizant of the difference between temporary and permanent cysts. Many instances among protozoa might be cited of the wide difference existing in the two types and in the same species, and Schaudinn and others have previously called attention to these differences in the parasitic rhizopods. Hence the cyst, as a feature in the identification of species as Walker gives them, loses it value. Walker's long list of species finally, while a convenient summary of the described amœboid parasites, can not be accepted as established, and his several "new" species must share the same fate, for in no case has the full life history—the only adequate basis of species—been made out. When the full history is worked out, these many so-called species will probably be reduced to mere varieties, or to a few species of the genus Entamœba.

G. N. C.

EXPERIMENTAL ZOOLOGY

Regeneration.[1]—Professor Korschelt has brought together in compact, yet readable form, the more important results on regeneration and transplantation in animals and plants. No small amount of discrimination is required to put into 170 pages all the results so far obtained on regeneration both of animals and of plants; yet Professor Korschelt has shown unusual judgment in selecting the essential and typical results of the old and the recent work. Necessarily, much detail has been pruned away, yet the author has succeeded in bringing into proper correlation many widely scattered facts. The more theoretical and analytical sides of the problem occupy a very

[1] Regeneration und Transplantation. By E. Korschelt. 1907.

secondary place in the present treatise, yet have by no means been entirely left out of account. We venture to think, however, that the more valuable outcome of the experimental study of regeneration lies less in a descriptive account of what takes place than in the attempt to give an analysis of the problems involved.

The second half of the book, some 75 pages, deals with Transplantation, or grafting, as it is more generally called. The more limited data in this field receive ample consideration.

The extensive literature of both subjects is arranged under topical headings—an arrangement that will recommend itself in the present case as preferable to the more usual methods of giving selected bibliographies at the end of each chapter or *en bloc* at the end of the book. We can not refrain, in passing, from calling attention to a slight misprint in one of the English titles that reads "The international factor in the regeneration of the tail of the tadpole."

Passing to a more detailed examination of Professor Korschelt's book, we find that while the formation of new growths in plants—more especially those cases where the new growth does not come from latent buds—is included under the heading of regenerative processes, the development of parts of the egg and the regulative changes that take place in isolated blastomeres and in fragments of the segmented egg are not included, despite the fact that the restoration of the whole form by a nucleated piece of a protozoon is described in some detail. Such limitations of the subject are, in the opinion of the reviewer, rather arbitrary; for, while it is unquestionably advantageous to limit certain fields, and to bring together certain groups of more closely related subjects, the fundamental problems of regeneration involved in all cases where a part produces a new whole have so much in common that the study of the subject gains rather than loses by taking as broad and as general an aspect of the subject as possible.

The most recent work on the regeneration of entire plants from leaves, as illustrated by the work of Goebel, Hildebrand, Winkler, Vöchting, Nemeč, Figdor and others is given in some detail in the opening chapter. It is pointed out that in many of these cases the new plant does not come from preformed buds, and not even from merismatic tissue in the case of Drosera according to Winkler, but directly from one or more cells of the epidermis of

the leaf. The problem of localization of the new growth in such cases is not discussed, nor have we, in fact, as yet any sufficient clue to the matter.

The growth of broken crystals in saturated solutions is dwelt on at some length. The remarkable similarity of this process to regeneration in organisms is emphasized, more especially in the light of the remarkable work of Lehman on fluid crystals. The author apparently suspends judgment concerning the interpretation of the resemblances of the two processes—whether we are dealing with only an analogous process or whether the two phenomena have fundamental properties in common. "Das Für und Wieder kann hier nicht erörtert werden."

Korschelt thinks that the loss of power to regenerate is a general accompaniment of the degree of organization (Organizationshöhe), yet he points out that this is not universal, as shown by the absence to regenerate in some forms and its presence in other closely related ones. In fact, the time-honored statement of such a relation has very little weight in the face of recent facts to the contrary. When, for example, such a complex organ as that of the eye of a salamander can regenerate from a piece of the bulb, while the head of the planarian, Dendrocoelum, fails to regenerate behind a certain level (where no obvious change in Organizationshöhe is apparent) we may well hesitate to lay any especial emphasis on such a generalization.

The discussion of the phenomenon of regeneration as an adaptation occupies only seven pages of the book. By adaptation is meant in general not so much that the process is useful—a fact too evident to dispute—but that *in some way* regeneration has been acquired on account of its usefulness. Our author would not, of course, adopt a teleological explanation, but assumes instead the supposed alternative of the Darwinian explanation of the origin of usefulness. Most students of the subject have rejected this interpretation on what the reviewer believes to be sufficient evidence. Korschelt's somewhat cautious attitude is summed up in the following statements. "Despite all the difficulties that have been raised one can not escape the impression that the power to regenerate and the liability to regenerate stand in a causal relation to each other." "We find that it is also the opinion of competent botanists that the interpretation of regeneration as an adaptation is little to the point. They agree with the zoologists mentioned above in this regard."

"If we look upon the power to regenerate as a property immanent in the living substance, which seems not improbable, owing to its wide occurrence, we may still suppose that this property has within certain lines of evolution been strengthened by adaptation and selection."

The origin of the new material from the old, the process of transformation (morphallaxis), the curious phenomenon of compensatory regulation, the occurrence of polarity and the development of heteromorphic structures are adequately dealt with from an objective standpoint, although in our opinion all too briefly considering the importance of the theoretical problems involved. These parts of the book are followed by a discussion of the factors of regeneration. The nature of the subject and the uncertainties of the theoretical problems involved make it difficult to treat such theoretical questions briefly and definitely, yet one could have wished that so admirable a review and so judicious a treatment of the descriptive processes might have been followed up by a more illuminating or at least suggestive discussion of the fundamental problems of regeneration as the title of this section might lead one to expect.

Under the heading of transplantation the grafting processes in plants is first briefly described. The important and recent results of grafting in animals receive careful attention. The interesting experiments on hydra by Wetzel, Rand, Peebles and King are sympathetically considered, and the equally important work of Korschelt's pupils, Joest and Rabes, are clearly and forcibly dealt with. Born's classical experiments with tadpoles, that have led to so many far-reaching experiments in recent years, occupy, as is their due, an important place in this field. The later work of grafting in amphibians, especially that of Harrison and Spemann, is described; but the author, while referring briefly to the important experiments of Lewes, has failed, in our opinion, to give them their proper place.

The author considers in some detail the modern work of transplantation of small portions of the tissues and has brought together in readable form the results of the literature of the subject, that is widely scattered, often in journals little accessible to zoologists. Korschelt's review will prove a useful source of information in such matters.

We cordially recommend Professor Korschelt's book as one of the most recent, most judicious and fair presentations of the

subjects of regeneration and grafting. The yearly reviews of Barfurth in the *Ergebnisse für Anatomie und Entwickelungsgeschichte* will supply special students with the numerous details that the study of regeneration is bringing to light. The more analytical and philosophical discussion of the problems involved will be found in the recent reviews and writings of Driesch. The general reader and layman who is less concerned with these details or with "the higher criticism" can not do better than give Korschelt's book a careful reading.

M.

PARASITOLOGY

A Chinese Parasite.—Looss has recently demonstrated[1] that under the old name *"Opisthorchis sinensis"* two human parasites have been confused by all save Baelz, whose differentiation of the two species in 1883 has been generally disregarded. For these forms the new genus Clonorchis is created with *C. sinensis* (Cobbold, 1875) as type. This species is the *Distomum inocuum* of Baelz and is chiefly a Chinese parasite, though it occurs rarely also in Japan. The other species is the *Distomum endemicum* of Baelz, which now becomes *C. endemicus;* it is the form usually described in text-books, etc., as *"Opisthorchis sinensis."* According to existing records it is very common in Japan and presumably so in Annam and Tonkin also. It seems to be confined to localities on the sea-shore. I would suggest that this appears to indicate infection through fish, as is the case with *Opisthorchis felineus* in the territory adjacent to the Baltic.

H. B. W.

[1] *Ann. Trop. Med. and Par.*, 1, 123.

(No. 497 was issued on June 7.)